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Identifying Pollution Related Changes in Chironomid Communities as a Function of Taxonomic Rank[1]

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Waterhouse, J. C., and M. P. Farrell. 1985. Identifying pollution related changes in chironomid communities as a function of taxonomic rank. Can. J. Fish. Aquat. Sci. 42: 406–413.

This study compares specific- and generic-level analyses of chironomid presence/absence data along a heavy-metal gradient. Eighteen binary similarity coefficients were calculated for five sampling stations from a small Ohio stream that receives an effluent containing zinc, copper, and chromium from a metal-plating industry. In general, the specific- and generic-level values were highly correlated and showed similar patterns across the 10 station comparisons. The basis for this correlation was then investigated by an assessment of both the amount (average number of species per genus) and the pattern (species to genus ratio trend) of information loss along the pollution gradient. Trends in the species to genus ratio along the gradient are viewed as indicative of the similarity of congenerics in their response to the gradient. The lack of a significant trend in the species to genus ratio in our data indicates that the agreement between specific- and generic-level analyses was due to the ability of a robust species distribution pattern to withstand a limited amount of random information loss, rather than any inherent similarity among congenerics reflected in their species to genus ratio trends. Analyses based on only a few species (e.g. abundant or indicator species) cannot afford as much information loss and must rely more heavily on similarity of congeneric species.

La présente étude porte sur une comparaison d'analyses de données (genre et espèce) sur la présence ou l'absence de chironomidés en fonction d'un gradient de métaux lourds. Dix-huit coefficients de ressemblance binaires ont été calculés pour cinq stations d'échantillonnage dans un petit cours d'eau de l'Ohio où sont déversés des effluents d'une usine de revêtement électrolytique, qui contiennent du zinc, du cuivre et du chrome. En général, les valeurs aux niveaux générique et spécifique étaient en corrélation étroite et suivaient des schèmes semblables quand on comparait les 10 stations. On a alors étudié cette corrélation en évaluant la quantité (nombre moyen d'espèces par genre) et la répartition (tendance du rapport espèce:genre) de l'information perdue le long du gradient de pollution. On considère que les tendances du rapport espèce:genre le long du gradient sont indicatives de la ressemblance des congénères pour ce qui est de leurs réactions au gradient. L'absence d'une tendance significative dans le rapport espèce:genre indique que la concordance entre les analyses aux niveaux spécifique et générique était due à la capacité d'un schème solide de répartition des espèces de résister à la perte limitée d'information aléatoire, et non à une ressemblance inhérente entre les congénères qui serait révélée dans les tendances du rapport espèce:genre. On ne peut se permettre une telle perte d'information dans le cas d'analyses basées sur quelques espèces (c.-à-d. des espèces abondantes ou indicatrices) ; on doit plutôt compter sur la ressemblance des espèces congénères.

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One of the most recurrent problems faced by ecologists is the difficulty of replacing subjective comparisons of species lists with objective numeric values summarizing the similarity among the communities. Many analytical techniques have been suggested to evaluate species check lists. However, many of the qualitative methods based on binary data have been ignored by ecologists because species abundance data are thought to be superior to species presence/absence data for comparing ecological communities (Grieg-Smith 1964; Clifford and Stephenson 1975). Recent studies using binary data have been successful in detecting patterns of change in ecological communities (Green 1979; Peterson 1976; Polovino et al. 1982; Allen 1971). Results of these studies indicate that qualitative data are not inferior to quantitative data but rather answer questions at a different level of resolution (Allen and Starr 1982).

When samples are to be compared on the basis of the organisms present in each, it is usually assumed that species-level identification is necessary for adequate evaluations. However, for some organisms, such as immature aquatic invertebrates, species identification may be difficult, unreliable, or impossible. Because this taxonomic confusion is frequently the case, species distribution patterns often must be derived from generic or mixed species/generic data. The objective of this study was to investigate the conditions under which generic-level data adequately represent species distribution patterns.

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[1] Publication No. 2461, Environmental Sciences Division, Oak Ridge National Laboratory.

Methods

To approach this problem, we compare the patterns shown by specific- and generic-level binary similarity coefficients calculated from the distribution of chironomids along a heavy-metal pollution gradient in a small Ohio stream. We then develop a theoretical framework based on the species to genus ratio to examine the ecological relevance of the generic groupings.

The data on chironomid communities were obtained from Elam's run, a second-order limestone stream in southwestern Ohio that receives a complex heavy-metal effluent from a metal-plating industry. A detailed description of the study area and sampling methods has been published previously (Winner et al. 1980). Briefly, samples were taken from five shallow riffle areas at varying distances from the source of effluent. Occurrence of 57 chironomid species was determined at each station using both box and emergence samplers. All species identifications were based on adults, either from field specimens or from larvae reared in the laboratory. Species abundances were obtained for adults collected in emergence traps. Copper, zinc, and chromium concentrations were monitored to assess chemical pollution gradients.

Eighteen binary similarity coefficients were chosen from the literature (Clifford and Stephenson 1975; Boesch 1977; Sokal and Sneath 1963; Lamont and Grant 1979) and calculated for each two-way comparison of species lists for specific- and generic-level data (Fig. 1). Values used to calculate binary similarity coefficients are as follows: A = conjoint presences; B = species present in first station but not second station; C = species present in second station but not first station; D = species absent in both stations being compared but present at one of the other three sampling stations. Correlations between specific- and generic-level binary similarity coefficients were calculated, and we used plots of the data to compare the patterns shown by specific- and generic-level values.

The rarefaction technique was used to calculate the number of genera (G) expected for a random sample of S species from a species pool consisting of all species sampled at the five stations. Formulas for the expected number of genera and its variance have been previously published (Hurlbert 1971; Simberloff 1978) as has been a Fortran program that provides the necessary results (Simberloff 1978). Differences between actual and expected numbers of genera at each of the five stations were tested using the z statistic corresponding to a normal distribution. The finite population correction term was included in the calculation of the variance because of the large sample size relative to the species pool. The normal distribution was assumed to be an adequate approximation within the range of sample sizes used.

Results and Discussion

Trends Along the Heavy-Metal Gradient

Heavy-metal concentrations showed a downstream decline with increased distance from the heavy-metal source. Copper, for instance, had mean levels of 336, 237, 221, 87, and 74 μg/L for stations 1 through 5, respectively. Although the concentration differences were not statistically significant because of extreme variability, there were clear downstream changes in the percentages of caddisflies and chironomids as well as changes in the chironomid species list (see Winner et al. 1980). The number of species per station increased with increasing distance below the point of metal introduction (Table 1). An exception to this trend is station 2, which is closer to the pollution source than station 3, but has more species (Table 2). Species relative abundance data also indicate this reversal in the expected ordering (Fig. 2). This reversal may be due to a 40% decrease in average current velocity from station 2 to 3, which may result in pulses of heavy-metals persisting for longer intervals at station 3 than at station 2 (R. W. Winner, Miami University, Oxford, OH, pers. comm.). We have altered the station ordering in our presentation of results to coincide with what appears to be the more biologically relevant gradient. Other interpretations of these data are possible and further study would be necessary to determine all the factors producing the species distribution, hence the apparent station orderings. Since our purpose was to compare species- and genus-level similarity analyses, we do not deal further with the problem of precisely determining the "correct" pollution ordering. Our basic conclusions hold regardless of the ordering of stations 2 and 3.

Comparison of Specific- and Generic-Level Coefficients

Comparing patterns shown by species- and genus-level data for values A, B, C, and D and the 18 binary similarity coefficients plotted against the 10 station comparisons (Fig. 1) shows that most of the similarity patterns are in good agreement for specific- and generic-level data because the peaks and depressions generally coincide.

This agreement in overall patterns conflicts with the results of correlations between specific and generic values for some of the coefficients (Fig. 1). This conflict is probably due to correlation analysis reflecting differences in specific- and generic-level coefficients that do not disrupt the overall pattern seen in these graphs. Generally, lower correlations were found for binary similarity measures that either use D in the numerator or do not use all three presence values (A, B, and C).

One might expect to find good agreement in the pattern shown by specific- and generic-level coefficients because the values of A, B, C, and D from which the coefficients were calculated also show similar patterns at the two levels. Futhermore, coefficients that showed lower correlations might be considered less appropriate for ecological data. In general, these coefficients either included conjoint absences (D) in the numerator or did not include all three presence values, A, B, and C (Fig. 1b). Our findings concur with theoretical considerations that recommend omitting conjoint absences (D) from calculations of station similarity (Goodall 1973; Clifford and Stephenson 1975).

Despite the overall similarity in pattern, we would caution that differences between specific- and generic-level patterns are probably sufficient to generate different station orderings if sensitive ordination techniques are used. However, with known inherent variability and the higher sampling error involved with detecting the presence of very rare species, it seems unlikely that these small differences in the patterns of the binary similarity coefficients are biologically or statistically significant. Therefore, discussions of binary similarity coefficient patterns in high variability situations such as this should not treat small changes in coefficient values as biologically meaningful. An alternative approach, which appears to reduce this problem, is the ordering of stations by the number of taxa. Such a richness index is less susceptible to chance variation because it more effectively integrates small-scale information specifying which species were found at a station. This approach is most appropriate in situations such as ours, where the relevant ecological change is successive deletions of taxa.

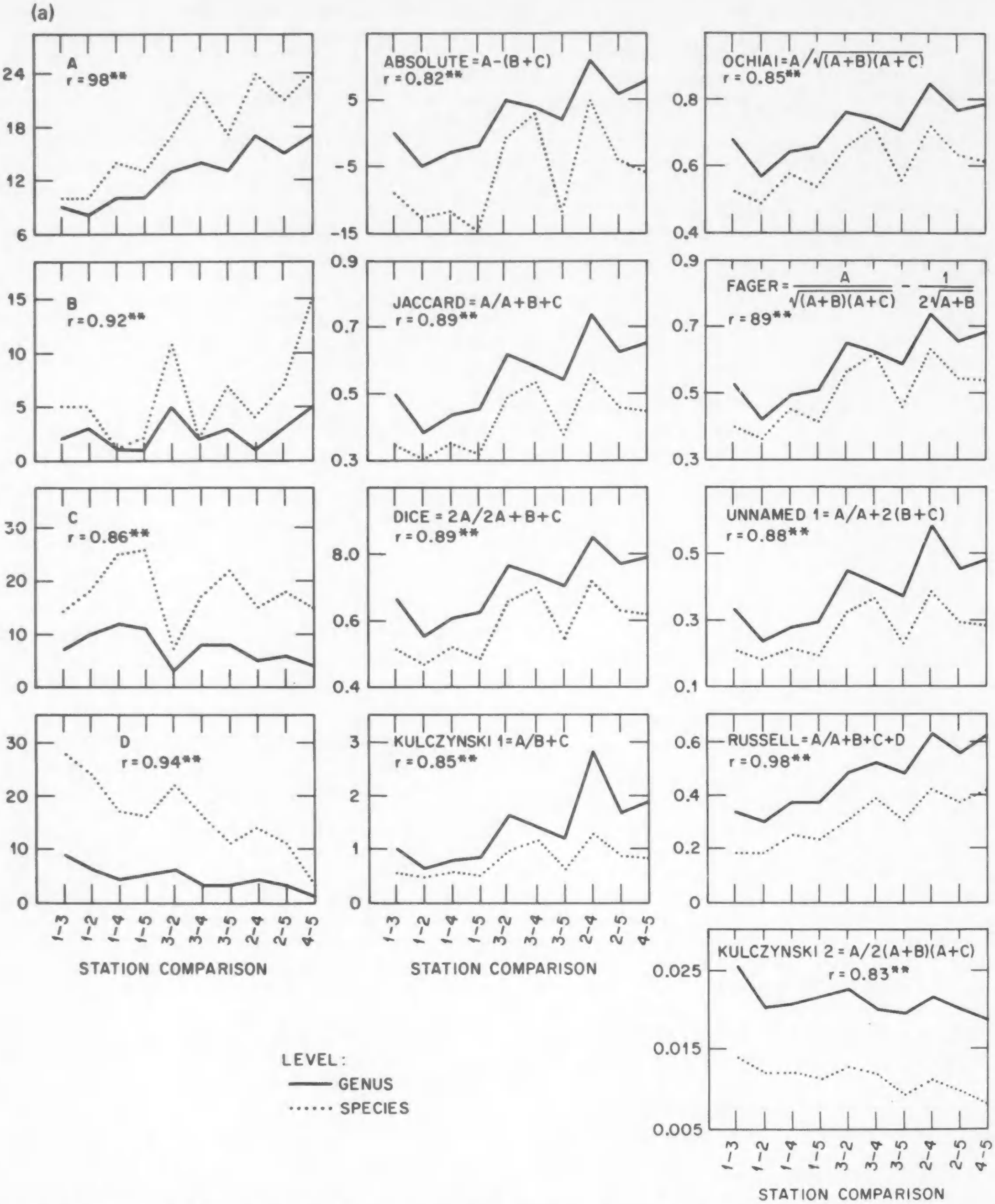

FIG. 1. Binary similarity coefficients for specific- and generic-level data plotted against station comparison. The correlation coefficient for the relationship between species and generic level values is presented ($*p < 0.05$, $**p < 0.01$). Figure 1a contains coefficients that lack D in the numerator and include all three presence values (A, B, and C). The coefficients in Fig. 1b either have D in the numerator or do not include A, B, and C.

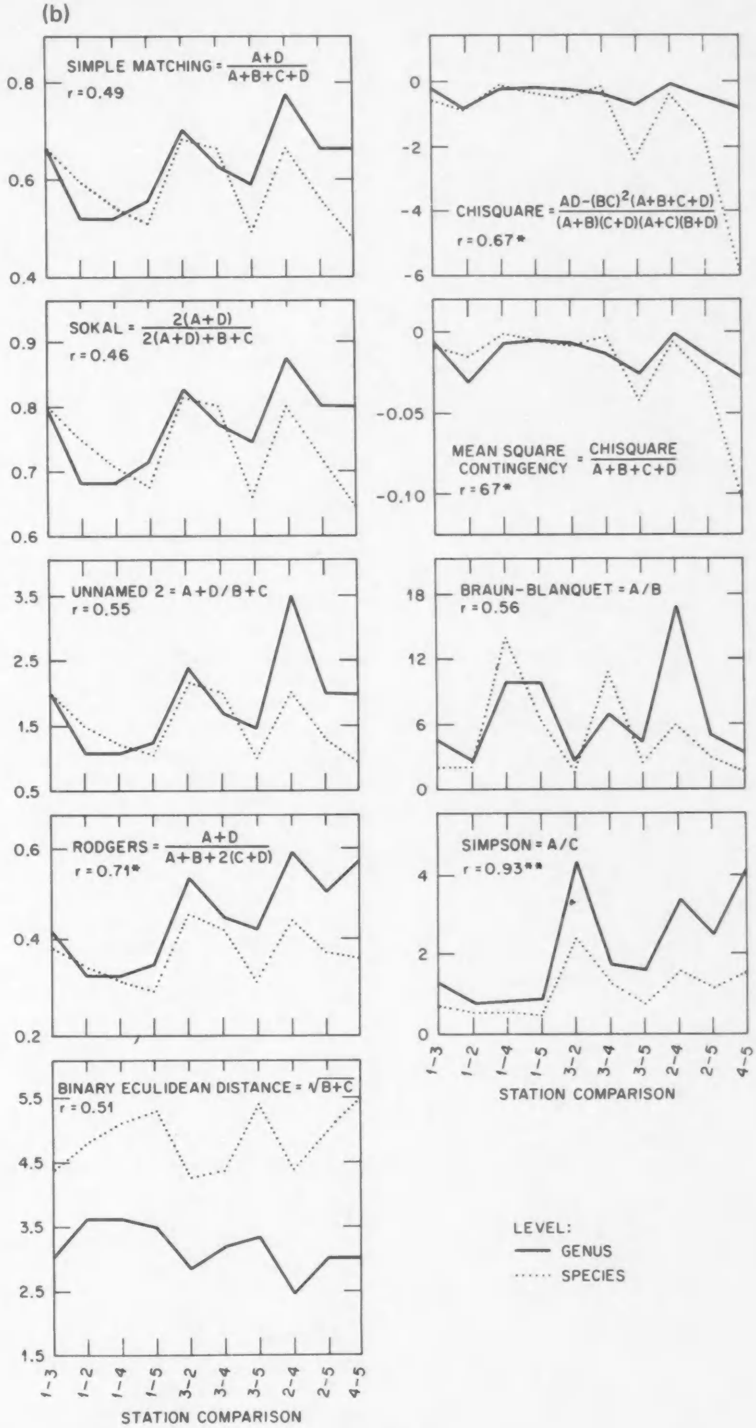

FIG. 1. (*Concluded*)

TABLE 1. Chironomid species list from Elam's run listed by genera in order of decreasing number of species per genus. Presence at the five sampling stations is indicated by +. (After Winner et al. 1980)

Species	Station 1	2	3	4	5
Pentaneura currani				+	
Pentaneura bifasciata		+		+	
Pentaneura fimbriata				+	
Pentaneura flavifrons		+		+	+
Pentaneura melanops	+	+	+	+	+
Pentaneura pilosella				+	
Pentaneura sinuosa	+	+	+	+	+
Pentaneura cornuticaudata					+
Cricotopus trifasciatus		+	+	+	
Cricotopus bicinctus	+	+	+	+	+
Cricotopus exilis	+			+	+
Cricotopus infuscatus	+	+	+	+	+
Cricotopus slossonae			+	+	
Cricotopus varipes		+	+	+	+
Metriocnemus aequalis					+
Metriocnemus atratulus					+
Metriocnemus exagitans					+
Metriocnemus lundbeckii	+		+	+	+
Orchocladius dubitatus	+	+		+	+
Orchocladius obumbratus		+	+	+	+
Orchocladius stamfordi					+
Orchocladius johannseni			+	+	
Tanytarsus dissimilis				+	+
Tanytarsus exiguus			+	+	
Tanytarsus neoflavellus		+	+	+	+
Tanytarsus viridiventris					+
Polypedilum convictum	+	+	+	+	+
Polypedilum halterale					+
Polypedilum scalaenum					+
Chironomus attenuatus	+		+	+	+
Chironomus riparius	+			+	
Cryptochironomus digitatus		+			+
Cryptochironomus fulvus		+	+	+	+
Dicrotendipes fumidus			+		+
Dicrotendipes neomodestus		+			
Eukiefferiella brevinervis		+	+	+	+
Eukiefferiella sordens		+	+	+	+
Larsia decolorata		+	+	+	
Larsia planensis		+			
Micropsectra deflecta		+	+	+	+
Micropsectra dives					+
Phaenopsectra flavipes		+			+
Phaenopsectra obediens				+	
Ablabesmyia monilis					+
Corynoneura scutellata	+	+		+	+
Cryptotendipes pseudotener				+	
Diamesa nivoriunda					+
Diplocladius cultriger		+		+	
Microtendipes pallidus				+	
Natarsia baltimoreus	+	+	+	+	+
Parachironomus tenuicaudatus			+		
Paratendipes albimanus	+				+
Procladius culciformis	+	+	+	+	+
Psectrotanypus dyari	+	+	+	+	
Stictochironomus flavicingula		+		+	+
Thienemanniella similis		+		+	+
Trichocladius nitidus				+	+

Assessing the Ecological Relevance of Generic Groups

To examine more closely the effect of using generic groupings, we calculated the number of species per genus at each station. An increase in the species to genus ratio with decreasing pollution effects was observed. The significance tests show, however, that the actual number of genera is not significantly different from that expected for a random sample of S species (Table 2).

These results are relevant to a consideration of the ecological significance of generic groupings. The acceptance of the null hypothesis shows that it is not necessary to attribute ecological significance to generic groupings of chironomid species to explain trends in the species to genus ratio along the heavy-metal gradient (Table 2). Two alternative hypotheses that imply similarity of congenerics may be considered (Table 3). One hypothesis predicts more species per genus at the more polluted stations, suggesting that many of the pollution-tolerant species belong to a few "pollution-tolerant genera." Our results do not support this hypothesis because congeneric chironomid species do not appear to be similar in their tolerance to heavy-metal concentrations (Tables 1 and 2). Resh and Unzicker (1975) also found little congeneric similarity in pollution tolerance for 61 aquatic macroinvertebrate genera. Other studies (Green 1979; Vascotto 1976) have suggested that congeneric species are similar on relatively large-scale habitat characteristics, with species differences occurring on a microhabitat scale. Although we did not observe this type of pattern at the scale of our study, it is possible that a study of larger scope might show that generic distributions reflect larger scale environmental features.

The other alternative hypothesis (Table 3) suggests that fewer species per genus should be found at the polluted stations (e.g. more monotypic genera). Reduced numbers of species per genus could result from reduced coexistence of similar competing congenerics in polluted areas. This is analogous to the interpretation of lower species to genus ratios on islands (Grant 1966; Williams 1964). The lack of this trend in our data does not preclude the possibility that competitive exclusion of chironomid species may increase with an increase in heavy-metal pollution. It may just be that congenerics are not particularly similar ecologically, and hence the basis for using changes in the species to genus ratio as an indication of competition no longer exists.

Each of the three possibilities for the ecological relevance of generic groupings (Table 3) is associated with an effect on the similarity indexes calculated at the generic level. If congenerics are similar in pollution response (the first alternative hypothesis), the generic-level analyses should be acceptable because

TABLE 2. Actual and expected values for the numbers of genera and the species to genus ratio. The difference between actual and expected number of genera is tested with the z statistic corresponding to the normal distribution. The variance of the expected number of genera is corrected for a finite population. ns = not significant at $\alpha = 0.05$.

		Species to genus ratio		Number of genera			
Station number	Number of species	Actual	Expected	Actual	Expected	Variance of expected number of genera	z
1	15	1.36	1.31	11	11.45	1.17	−0.38 (ns)
3	24	1.50	1.50	16	16.04	1.24	−0.03 (ns)
2	28	1.56	1.57	18	17.78	1.18	0.19 (ns)
4	39	1.77	1.78	22	21.86	0.86	−0.99 (ns)
5	39	1.86	1.78	21	21.86	0.86	0.17 (ns)

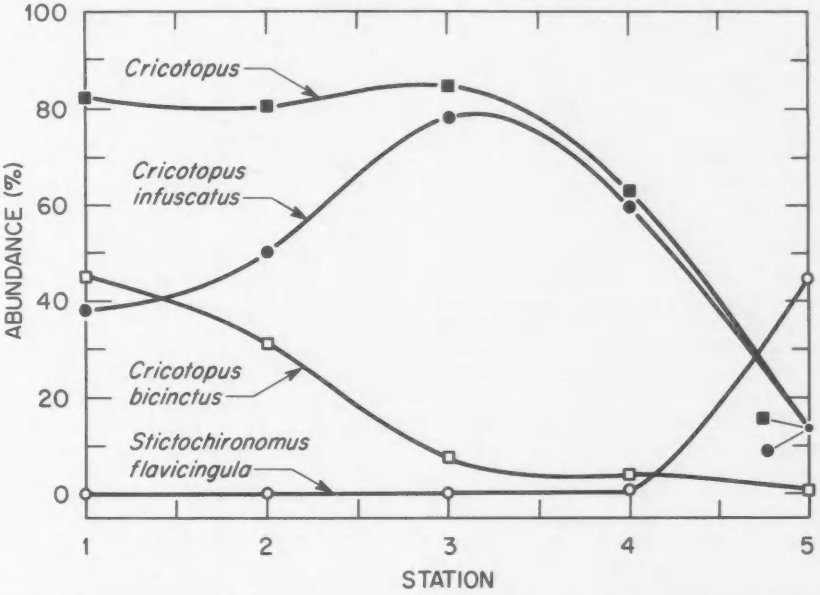

FIG. 2. Proportional abundances of the three dominant chironomid species plotted along a heavy-metal gradient (see text for comment on station ordering). *Cricotopus* refers to the combined abundances of *C. infuscatus* and *C. bicinctus*.

only redundant information is lost. The second alternative hypothesis suggests a tendency for stations to have similar genera, with any differences attributable to polluted stations having fewer coexisting congeneric species. This situation would result in a decreased ability for generic-level analyses to differentiate between stations.

The acceptance of the null hypothesis indicates that the actual effect on the binary similarity coefficients is a random loss of species information with the collapse to the generic level of taxonomic identification. The amount of information lost appears to be related to the number of species in each genus. Chironomid genera containing many species contribute little to the ability of the generic-level coefficients to differentiate between stations because at least one species is usually present at every station. In this study, two genera with six and eight species showed this effect. However, 13 of the 27 genera had only 1 species and 7 had only 2 species. Obviously, monotypic genera do not lose information when collapsed to the generic level, and genera with two species generally lost little information. In addition, many chironomid taxonomists would have split many of the genera in this study, resulting in more genera with fewer species per genus (M. W. Boesel, Miami University, Oxford, OH, pers. comm.). These changes would result in less information loss and even closer agreement between specific- and generic-level data.

Mixed specific and generic identifications should result in less information loss than generic-level data. However, patterns detected using binary data may be biased toward the patterns shown by taxa identified to species because they will contribute relatively more information to the analysis. Similar biases may occur when more than one person does the identifications, since taxa identified by "splitters" will also contribute more informa-

TABLE 3. Ecological relevance of generic grouping and consequence on binary similarity coefficients associated with three possible trends in the average number of species per genus.

Hypothesis[a]	Ecological relevance of generic grouping	Effect of using generic level on coefficient pattern
H_0: S/G is similar to number expected by chance	None, or mixture of opposing effects (i.e. H_1 with and H_2) neither effect predominating	Some loss of information but adequate if S/G not too high
	Two alternatives	
H_1: S/G at more polluted stations greater than expected by chance	Indicates similarity among congenerics in pollution response (i.e. "pollution-tolerant genera")	Generic level similar to species level or may show a larger scale pattern if generic similarity is on a grosser scale
H_2: S/G at more polluted stations less than that expected by chance	Competition between ecologically similar congenerics reduces their ability to coexist in polluted areas	Generic level should be less effective in showing station differences

[a] S/G = mean number of species per genus at a station.

tion to the analysis. Naturally, identification to only the family or order level results in greater potential for loss of species distribution information. Examination of the amount and pattern of information loss along environmental gradients could be undertaken in other data sets in a manner analogous to that used here (e.g. using species to family or species to order ratios) to determine what effect higher level analyses will have on pattern detection.

Kaesler et al. (1978) used hierarchical diversity indexes (which calculate components of the total diversity attributable to different taxonomic levels) to show that the amount of information lost by using higher taxonomic levels may not be sufficient to necessitate species-level identification. Our approach indicates that not only the amount but the pattern of information loss along a gradient may be important for gradient detection. This pattern of information loss (species to genus ratio trend) is determined by the similarity of congenerics in their response to a particular environmental gradient. Thus, both the type of organism and the environmental gradient considered may have an effect on the pattern of information loss and hence the utility of higher taxonomic levels in gradient detection.

It should also be stressed that the robustness of the pattern to be detected is an important consideration for the determination of the appropriate level of identification. A very fine-scale gradient may require specific-level analyses, while relatively coarse gradients may be detectable at the generic, family, and even order level of classification.

Use of Abundance Data

Caution should be used in extrapolating these results to other types of coefficients or evaluations. For example, conclusions as to the effect of using generic-level taxonomic identification appear to be different when abundance data are used. When the three most abundant species are plotted along the heavy-metal gradient (Fig. 2), the stations can be easily differentiated. However, when the generic level is used, two of the dominant species are combined so that their changing abundances cancel out, and the analysis no longer differentiates among stations 1 through 4. Therefore, for approaches that rely heavily on the abundances of a few dominant species (i.e. evenness indexes, quantitative coefficients, and indicator species approaches), it appears that the use of the generic level could lead to serious biases. These approaches do not have the advantage of using many species that on the average may retain the general similarity pattern even after information is lost at random through the collapse to the generic level. Because quantitative indexes are generally sensitive to a few dominant species, they require similar pollution tolerance characteristics of congenerics to adequately represent species distribution patterns. These assumptions, at least for the response of congeneric chironomid species to heavy-metal pollution, are not supported.

The difference in conclusions for abundance and qualitative data may partially resolve the apparent disagreement in the literature regarding the adequacy of higher taxonomic levels. Studies using diversity indexes (Kaesler et al. 1978; Hellawell 1978) have indicated that the generic or family level may often be adequate, while studies emphasizing indicator species, bioassay procedures, and rare species detection (Resh and Unzicker 1975; Resh 1979) stress the need for species identification. Although diversity indexes may be influenced by dominant species, they also include the effect of numerous other species through the richness component, and thus may be better able to withstand information loss. As Resh (1979) noted, the use of higher taxonomic levels will probably result in an underestimation of species diversity; however, this is unlikely to be a problem for studies that compare diversities with the same level of taxonomic resolution.

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A General Theory for Analysis of Catch and Effort Data

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This paper presents a general theory for analysis of catch and effort data from a fishery. Almost all previous methods are shown to be special cases, including those of Schaefer, Pella and Tomlinson, Schnute, and Deriso, as well as the stock reduction analysis technique of Kimura and Tagart and Kimura, Balsiger, and Ito. Like that of Deriso, the theory here is based on natural equations for an age structured population. However, instead of a fixed single model, this paper gives a general model that can be tailored to any particular fishery. The problem of determining the appropriate special case is conceptually identical to the model identification problem described by Box and Jenkins in the context of time series analysis. Identification necessarily begins with a suitable class of models. This paper defines such a class, unique to fisheries, complete with mathematical proofs and biological explanations of all important equations.

Le présent article porte sur une théorie générale pour l'analyse des données sur les prises et l'effort. L'auteur démontre que presque toutes les anciennes méthodes sont des cas spéciaux, y compris celles de Schaefer, de Pella et Tomlinson, de Schnute et de Deriso, ainsi que la technique d'analyse de la réduction des stocks de Kimura et Tagart et de Kimura, Balsiger et Ito. Comme celle de Deriso, la présente théorie est basée sur des équations naturelles pour une population à structure d'âge. Toutefois, au lieu d'un seul modèle fixe, le présent article décrit un modèle général qui peut être adapté à une pêche donnée. La détermination du cas spécial approprié pose un problème essentiellement identique au problème de détermination d'un modèle que mentionnent Box et Jenkins relativement à l'analyse de séries chronologiques. Le processus commence forcément avec une classe adéquate de modèles. Le présent article définit une telle classe, particulière aux pêches, avec les preuves mathématiques et les explications biologiques de toutes les équations importantes.

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A fundamental problem of fishery management is to deduce the state of a stock from the historical record of catches and fishing efforts. The literature contains numerous proposed methods for solving this problem, including those of Baranov (1925), Thompson and Bell (1934), Schaefer (1954, 1957), Pella and Tomlinson (1969), Walter (1973), and Schnute (1977). Concurrent with these developments, various critics have debated the validity of the results. For example, Skud (1975) documented a lengthy debate prompted by Burkenroad's (1948) claim that the fishery was not the dominant influence on halibut (*Hippoglossus stenolepis*) stocks. In a more theoretical vein, Uhler (1980), Ludwig and Walters (1981), Walters and Ludwig (1981), and Ludwig and Hilborn (1983) pointed out problems with the statistical analysis of models based on data measured with error and suggested various methods to overcome these problems.

Deriso (1980) gave a remarkably fresh approach to this basic problem by showing that a composite model for catch and effort data can be derived mathematically from an age structured model of the Beverton–Holt type (Beverton and Holt 1957). Since fish populations, at least in northern and temperate climates, are composed of distinct annual cohorts, Deriso's result ties together biology and theory in a very neat way. Practitioners became enthusiastic; for example, Walters (1980) publically complimented Deriso for "what may be the most important contribution of fisheries population theory in the last two decades." As people began to apply the method, however, enthusiasm waned somewhat. For example, Roff (1983) investigated a simple ad hoc model which gave predictions as good or better than the methods of either Deriso (1980) or Schnute (1977).

Even if Deriso's method performs poorly in practice, it has considerable value as a theoretical and conceptual tool. Earlier models, such as those of Schaefer (1957) and Schnute (1977), are based on theoretical properties of how a population limited in size by its environment ought to perform. Models of the Deriso type have a more solid footing. Among other things, they reflect the undeniable reality that the population consists of cohorts that get one year older each year. Thus, even if they serve only as a guide to intuition, they have value to the practitioner. Part of my intent in this paper is to enlarge the framework of understanding such models so that they serve as better tools for conceptual thinking.

The diverse and conflicting literature on this subject raises a fundamental question: "Which model is right?" In fact, fisheries scientists are not the first to ask such questions. Catch and effort data fall into the general class of time series data, and statisticians have long pondered the problem of determining useful time series models. Box and Jenkins (1970) not only proposed a very general model, but also described a philosophy for tackling the fundamental question just cited. Their strategy (1970, p. 18–19) involves four steps, paraphrased below:

Step 1. From the interaction of theory and practice, postulate a useful class of models appropriate to the situation. A typical model in the class may potentially involve a large number of parameters.

Step 2. Use data and a knowledge of the system to identify a particular tentative model from the class. This involves restricting the model parameters in a meaningful way.

Step 3. Estimate the parameters in the tentative model of step 2.

Step 4. Perform diagnostic checking. Is the tentative model adequate? If not, return to step 2 and revise accordingly. If so, use the model for forecasting and control.

Much of the debate on fisheries models stems from a failure to come to terms with step 1. The important concept here is a *class* of models. If we are to decide which model is right, then we must be able to compare the candidates; consequently, the candidates themselves must all be special cases of some general class. For example, Box and Jenkins (1970) proposed the class of ARMA (autoregressive moving average) models for time series. Their step 2 consists in deciding how many lagged terms should be included in the autoregression and moving average. Revision in step 4 involves either increasing or reducing the number of terms in the model. At the end of the process, all models entertained are comparable because they fit into the unified class postulated in step 1.

By contrast with the situation for ARMA models, consider, for example, the models of Schnute (1977), Deriso (1980), and Roff (1983). Schnute's model is based on one theory, Deriso's on another theory, and Roff's on an ad hoc assumption. To compare them is, in the proverbial sense, to compare apples and oranges. Of the three models, however, Deriso's clearly best follows the spirit of step 1 above. More than the others, it is based on biological theory and practice; consequently, it is most likely to be useful for making decisions related to fish biology.

In this paper, I derive a class of models for analysing catch and effort data, based on assumptions of the Deriso type. My main object is to make the model building strategy of Box and Jenkins (1970) at least potentially achievable by completing the first step: postulating a useful class of models. I do not believe that the general ARMA model is appropriate in this context because it is not derived from biological theory. Furthermore, ARMA models are linear, although recruitment is an inherently nonlinear process (otherwise populations would be either infinite or extinct). The biologically motivated class described here turns out to include the models of Schaefer (1957), Pella and Tomlinson (1969), Schnute (1977), Deriso (1980), and Roff (1983) as special cases. Consequently, it becomes possible to compare them, apples to apples, as it were. Furthermore, many of the statistical problems described by various authors can be precisely identified in this new formulation.

In summary, the ideas given here have practical implications for the whole technique of fishery modelling. The modeller does not simply apply a universal model for all catch and effort data. Instead, he or she (step 1) uses a general framework for constructing such models, with enough flexibility to accommodate a wide range of biological assumptions. The modeller's task is then (step 2) to identify those particular assumptions that apply to the case at hand, (step 3) to fit these into the general framework, and thus to build an appropriate model for the stock in question. Since biological assumptions are often tenuous, it may typically be reasonable (step 4) to build several related models and to compare the results. The advantage of a universal framework is that the various results are then easily comparable, since all can be considered special cases of a larger whole.

1. The Model

1A. Notation and Assumptions

A consistent notation is important for stating the model and its consequences properly, particularly since the model involves numerous mathematical objects. There are two basic measures of time (in years): age a and year t. It is assumed that there is a fixed age k at which fish are recruited to the fishery. Deriso (1980) called this "knife-edged" recruitment. In order not to detract from a few central features of the model, I have devoted this paper entirely to the knife-edged case, although a more general "incomplete recruitment" model similar to that discussed by Deriso could also be developed. Notice that a fish of age a in year t was born in year $t - a$ and recruited in year $t - a + k$. Some minor clarification may be needed here because fish (unlike humans) are not usually aged from their birthdate; furthermore, fish age is measured from the time of birth as an egg. In any particular fishery, there is a convention that defines the "start of the year." It may be January 1, but it may also be the time when the fishing season begins in the spring. A fish born the previous fall, for example, automatically becomes 1 yr old at this time, even though chronologically it is much less than 1 yr old. As a result of this convention, a fish of age a in year t has parents belonging to the mature stock in year $t - a$. In particular, the mature stock in year $t - k$ determines recruitment in year t.

The model involves three main functions of a and t: the total number of available fish (the population) N_{at} aged a at the start of year t, the number C_{at} caught at age a during year t, and the weight w_{at} of a single fish aged a in year t. Corresponding to the numbers N_{at} and C_{at} are the biomasses

$$\begin{aligned} N_{at}^* &= w_{at}N_{at} \\ C_{at}^* &= w_{at}C_{at}. \end{aligned} \tag{1.1}$$

Throughout this paper, a superscript asterisk distinguishes biomasses of fish from numbers of fish. The model also involves two functions of t alone: the recruitment R_t of fish of age k at the start of year t, and the fishing effort E_t during year t. Again, there is a related biomass

$$R_t^* = w_{kt}R_t. \tag{1.2}$$

Furthermore, corresponding to age structured populations, are the totals

$$\begin{aligned} N_t &= \sum_{a=k}^{\infty} N_{at} \\ C_t &= \sum_{a=k}^{\infty} C_{at} \end{aligned} \tag{1.3}$$

and related biomass totals

$$\begin{aligned} N_t^* &= \sum_{a=k}^{\infty} N_{at}^* \\ C_t^* &= \sum_{a=k}^{\infty} C_{at}^*. \end{aligned} \tag{1.4}$$

Definitions (1.3)–(1.4) reflect a convention used throughout this paper: when the first subscript a is dropped from a doubly subscripted quantity such as N_{at}, the resulting function of t refers to the sum over recruited ages.

In addition to the above functions of a and t, there are numerous parameters that drive the model. One of these is the recruitment (age k) weight V_t associated with the cohort born in year t and recruited in year $t + k$. This same cohort is assumed to have an extrapolated prerecruitment (age $k - 1$) weight v_t, and a Ford growth coefficient ρ. By definition of v_t and V_t:

$$\begin{aligned} v_t &= w_{k-1,t+k-1} \\ V_t &= w_{k,t+k}. \end{aligned} \tag{1.5}$$

In (1.5) the prerecruitment weight v_t should be interpreted as a parameter, rather than the acutal weight at age $k - 1$; for this reason it is called an "extrapolated" weight. The model simply uses v_t, V_t, and ρ as three parameters to define the growth curve for ages $a \geqslant k$. Typically, fish younger than age k have weights that do not conform to the mature growth curve. The model also involves a mortality parameter M_t and a catchability parameter q_t associated with natural mortality and fishing, respectively. These allow the definition of three fractions: natural survival σ_t, fishing survival ϕ_t, and total survival τ_t. Finally, there are three parameters α_t, β, and γ related to recruitment. This notation is summarized in Tables 1 and 2. Various parameters, such as M_t, are presumed to depend on t, rather than being constants, to allow stochastic behavior to be introduced systematically in the model. For example, variation in natural mortality can be accounted for by assuming that M_t is a random variable with mean M. Similarly, q_t, V_t, and α_t can be used to introduce random fluctuations in catchability, growth, and recruitment, respectively.

Using the above notation, the model consists of eight assumptions:

$$N_{a+1,t+1} = \tau_t N_{at} \tag{1.6}$$

$$C_{at} = [1 - \phi_t] N_{at} \tag{1.7}$$

$$N_{kt} = R_t\{N^*_{t-k} - C^*_{t-k}\} \tag{1.8}$$

$$w_{a+1,t+1} - w_{at} = \rho(w_{at} - w_{a-1,t-1}) \tag{1.9}$$

$$\tau_t = \sigma_t \phi_t \tag{1.10}$$

$$\sigma_t = \exp(-M_t) \tag{1.11a}$$

$$\phi_t = \exp(-q_t E_t) \tag{1.12a}$$

$$R_t\{S\} = \alpha_t S(1 - \beta\gamma S)^{1/\gamma}. \tag{1.13a}$$

The first three equations describe fish population dynamics, and the fourth describes growth dynamics. The next three give the particulars of survival from total, natural, and fishing mortalities, respectively. Finally, the last equation details the recruitment process. Equations (1.6), (1.7), and (1.9) all apply only to recruited ages $a \geqslant k$, with the understanding in (1.9) that, when $a = k$, the prerecruitment weight $w_{k-1,t-1}$ is extrapolated. In (1.8) and (1.13a), braces designate functional dependence; thus "$R_t\{S\}$" means that R_t is a function of S.

The model is constructed so that the last three equations can readily be modified without altering some of the main conclusions. For example, three alternatives to the pair (1.11a)–(1.12a) are

$$\sigma_t = \frac{M_t + q_t E_t}{M_t \exp(M_t + q_t E_t) + q_t E_t} \tag{1.11b}$$

$$\phi_t = \frac{M_t + q_t E_t \exp(-M_t - q_t E_t)}{M_t + q_t E_t} \tag{1.12b}$$

or

$$\sigma_t = \{1 + \exp(q_t E_t)[\exp(M_t) - 1]\}^{-1} \tag{1.11c}$$

$$\phi_t = 1 - \exp(-M_t)[1 - \exp(-q_t E_t)] \tag{1.12c}$$

or

$$\sigma_t = \exp(-M_t) \tag{1.11d}$$

$$\phi_t = 1 - q_t E_t. \tag{1.12d}$$

An alternative to (2.13a) is

$$R_t = R \tag{1.13b}$$

where R is a constant. The significance of each model assumption, including the various alternatives, is described in the paragraphs following.

TABLE 1. Notation for the primary quantities that define the model (1.6)–(1.13). A dimensionless quantity is indicated by a dash in the units column.

Notation	Meaning	Typical units
	Time	
a	Fish age	yr
t	Year of the fishery	yr
	Functions	
N_{at}	Population of age a fish at the start of year t	Fish
C_{at}	Catch of age a fish during year t	Fish
w_{at}	Weight of a fish at age a in year t	kg
R_t	Recruitment at the start of year t	Fish
E_t	Fishing effort during year t	Boat-days
	Parameters	
k	Age of recruitment	yr
M_t	Instantaneous natural mortality in year t	—
q_t	Catchability in year t	1/(boat-days)
v_t	Prerecruitment weight of a fish born in year t	kg
V_t	Recruitment weight of a fish born in year t	kg
ρ	Ford's growth coefficient	—
α_t	Recruitment productivity parameter	Fish/kg
β	Recruitment optimality parameter	1/kg
γ	Recruitment limitation parameter	—

1B. Population Dynamics

The first assumption (1.6) summarizes the process of aging one year. For age $a \geqslant k$, the cohort population N_{at} at the start of year t is simply multiplied by the total survival fraction τ_t to obtain number of fish remaining in this cohort at the start of the next year. Similarly, if ϕ_t represents the fraction of the population that survives fishing, then (1.7) expresses catch C_{at} as the complementary fraction $1 - \phi_t$ of the cohort population. The most important aspect of both these assumptions is that survival does not depend on age after the recruitment age k. This will be true if both natural and fishing mortality are age-independent. Although constant natural mortality is a rather common assumption, the requirement that catchability should not vary with age is more severe. As mentioned earlier, the model assumes that fishing gear has knife-edged selectivity for recruited versus nonrecruited fish. Thus, the model does not include a more general selection ogive (Beverton and Holt 1957, p. 75–82; Fournier and Archibald 1982, p. 1198, equations 2.1 and 2.2), a restriction that is perhaps reasonable for the model's intended use on catch data without age information. At the price of

TABLE 2. Notation defined in terms of the model's primary quantities listed in Table 1. The number of the defining equation from the text is shown, along with typical units of measurement.

Notation	Equation	Meaning	Units
		Functions	
N^*_{at}	(1.1)	Population biomass at age a, start of year t	kg
C^*_{at}	(1.1)	Biomass at age a, caught in year t	kg
N_t	(1.3)	Total available population, start of year t	Fish
N^*_t	(1.4)	Total available biomass, start of year t	kg
C_t	(1.3)	Number of fish caught during year t	Fish
C^*_t	(1.4)	Biomass of fish caught during year t	kg
R^*_t	(1.2)	Biomass of fish recruited at the start of year t	kg
		Parameters	
ϕ_t	(1.12)	Survival from fishing mortality in year t	—
σ_t	(1.11)	Survival from natural mortality during year t	—
τ_t	(1.10)	Survival from all mortality during year t	—
W_t	(1.18)	Asymptotic weight of a fish born in year t	kg
K	(1.19)	Brody's growth coefficient	1/yr
$a_{0,t}$	(1.20)	Extrapolated age of 0 weight for birth year t	yr
R_m	(1.31)	Maximum possible recruitment	Fish
S_m	(1.31)	Stock for maximum recruitment	Fish
S_0	(1.32)	Carrying capacity	Fish

greater mathematical complexity, this assumption can be partly avoided (Deriso 1980, p. 271–273), but for reasons cited earlier, incomplete recruitment is not considered here.

The third equation (1.8) describes recruitment of age k fish in year t as a function of the post-fishing biomass in year $t - k$. The particular form of the function $R_t\{S\}$, where S is the stock biomass, is given in (1.13), one of the flexible assumptions identified earlier. The most important aspects of (1.8) are, first, that recruitment occurs at age k and, second, that recruitment depends on available biomass. If, for example, recruitment were to depend instead on available population (remove the two asterisks from (1.8)), then some of the model's main conclusions would change, as explained later.

1C. Growth

The fourth model assumption (1.9) is essentially Ford's (1933) growth model (Ricker 1975, p. 222, equation 9.17). Ricker refers to ρ as "Ford's growth coefficient." Typically, ρ is a fraction, $0 < \rho < 1$; thus, (1.9) states that the annual weight increment decreases by the factor ρ each year. Values of $\rho \geqslant 1$ are also possible, and the growth increment is constant when $\rho = 1$. When $\rho \neq 1$, it follows that

$$(1.14) \qquad w_{at} = v_{t-a} + (V_{t-a} - v_{t-a})\frac{1 - \rho^{1+a-k}}{1 - \rho}.$$

This is obtained by solving the difference equation (1.9), using the initial conditions (1.5) rewritten with different indices as

$$(1.15) \qquad \begin{aligned} w_{k-1,t-1} &= v_{t-k} \\ w_{kt} &= V_{t-k}. \end{aligned}$$

Schnute and Fournier (1980, appendix A) give a formal derivation. The reader can verify that (1.14) satisfies both conditions (1.15), and a proof also follows by mathematical induction. Consistent with earlier discussion, (1.14) applies only to recruited ages $a \geqslant k$; the prerecruitment weight v_{t-a} is merely a convenient parameter.

The growth equation (1.14) can be written in numerous alternative forms, using different choices of parameters. Two such alternatives are

$$(1.16) \qquad w_{at} = W_{t-a} - (W_{t-a} - V_{t-a})\rho^{a-k}$$

$$(1.17) \qquad w_{at} = W_{t-a}[1 - e^{-K(a-a_{0,t-a})}]$$

where

$$(1.18) \qquad W_{t-a} = (V_{t-a} - \rho v_{t-a})/(1 - \rho)$$

$$(1.19) \qquad K = -\log \rho$$

$$(1.20) \qquad a_{0,t-a} = k - 1 - \frac{\log [(V_{t-a} - v_{t-a})/(V_{t-a} - \rho v_{t-a})]}{\log \rho}.$$

The parameters in (1.18)–(1.20) are, respectively, the extrapolated asymptotic weight W of a fish born in year $t - a$, Brody's growth coefficient K (Ricker 1975, p. 221), and the extrapolated age a_0 when a fish born in year $t - a$ has weight 0.

The three growth curves (1.14), (1.16), and (1.17) are equivalent; the following table lists the parameters in each:

Equation	Parameters
(1.14)	v, V, ρ
(1.16)	W, V, ρ
(1.17)	W, K, a_0

Perhaps the most common form of the curve is (1.17), the von Bertalanffy equation (Ricker 1975, p. 221, equation 9.9). However, the form (1.14) is preferable here for two reasons. First, equations of the general theory below take the simplest form when (1.14) is used. Second, (1.14) is closely related to the growth model adopted by Deriso (1980, equation 1), namely

$$(1.21) \qquad w_{at} = w_{k,t-a+k}\frac{1 - \rho^{1+a-k}}{1 - \rho}.$$

Since $w_{k,t-a+k} = V_{t-a}$ by (1.5), this model is the same as (1.14) with the restriction

$$(1.22) \qquad v = 0.$$

From (1.20), (1.22) is equivalent to the requirement

(1.23) $a_0 = k - 1$

in the von Bertalanffy equation (1.17). Thus, Deriso's growth model extrapolates back to weight 0 at the prerecruit age $k - 1$, as can be seen directly by substituting $a = k - 1$ in (1.21).

Since growth is just one component of the general theory, Deriso quite reasonably decided to impose (1.22) (or, equivalently, (1.23)) for the sake of parsimony. In such a large model, the number of parameters quickly gets out of hand. Also, without (1.22), it seems impossible to complete the formulation of the incomplete recruitment model. Here, I am avoiding the latter problem, and I do not assume (1.22). This gives the general theory somewhat better symmetry, as shown below. Also, in at least some cases, (1.22) may be too restrictive. For example, consider a Pacific herring (*Clupea harengus pallasi*) sample taken from Yellow Point on the east coast of Vancouver Island, B.C., in March 1982. Fish are recruited dominantly at age $k = 3$ and mean weights (grams) for ages 3–8 turn out to be 95.27, 113.45, 130.99, 146.19, 170.43, and 175.38, respectively (Stocker et al. 1982, p. 102). Parameter estimates for a least squares fit to these data are listed below:

Model	v	V	ρ
(1.14)	73.4	94.5	0.925
(1.21)	0.0	76.9	0.553

Figure 1 shows the two growth curves in relation to the data. The constraint (1.23) that the curve should pass through 0 at age 2 (i.e. age $k - 1$) makes it difficult for the model (1.21) to capture the nearly linear trend in the data, particularly for the dominant ages 3–6. By contrast, notice that ρ is nearly 1 in the model (1.14).

1D. Mortality Details

The fifth model assumption (1.10) states that the total survival fraction is the product of survivals from fishing and natural mortality. Given the earlier equations (1.6)–(1.7) involving τ_t and ϕ_t, this apparently reasonable assumption really amounts to a definition of σ_t. A short algebraic calculation (Appendix A) based on (1.6), (1.7), and (1.10) shows that

(1.24) $N_{a+1,t+1} = \sigma_t(N_{at} - C_{at})$;

that is, σ_t represents the fraction of fish *not caught* in the fishery that survives to the next year. Fishing and natural mortality may occur concurrently; however, from (1.7), ϕ_t is the fraction of the original population that survives the fishery, and from (1.24), σ_t is the fraction of the remaining population that survives natural mortality.

The model is flexible as to the precise details whereby fishing and natural mortality occur. If fishing occurs first, in a pulse immediately following recruitment, then (1.11a)–(1.12a) describe the relevant survivals based on mortality M_t, catchability q_t, and effort E_t. If fishing and natural mortality take place simultaneously throughout the year (as assumed, for example, by Beverton and Holt 1957; Ricker 1975; Fournier and Archibald 1982; Kimura and Tagart 1982), then (1.11b)–(1.12b) apply. If pulse fishing occurs at the end of the year, just prior to recruitment, then (1.11c)–(1.12c) are correct. Appendix A justifies all three of these formula pairs. They have the common feature that the product $\sigma_t\phi_t$, the total mortality, in each case is

(1.25) $\tau_t = e^{-(M_t + q_t E_t)}$.

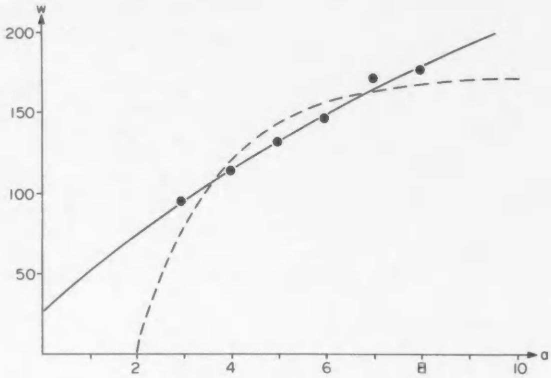

FIG. 1. Two growth curves for Pacific herring (*C. harengus pallasi*) from least-squares fits to data listed in the text. Recruitment is at age $k = 3$. Data points are shown as enlarged dots. The solid curve is based on the three-parameter model (1.14) with $(v, V, \rho) = (73.4\text{ g}, 94.5\text{ g}, 0.925)$. The broken curve is Deriso's two-parameter model (1.21) with $(V, \rho) = (76.9\text{ g}, 0.553)$, constrained to weight 0 at the prerecruitment age 2.

Deriso (1980) implicitly assumed none of the above three options, but rather (1.11d)–(1.12d). The expression (1.12d) for ϕ_t has the advantage that, from (1.7), it implies

$$C_{at}/E_t = q_t N_{at};$$

that is, catch per unit effort (CPUE) is proportional to the population. However, unlike (1.12a), (1.12d) also has the rather unreasonable feature that a finite effort, namely

$$E_t = 1/q_t,$$

will remove the whole population ($\phi_t = 0$). Consequently, (1.12d) is avoided throughout the rest of this paper in favor of one of the other assumptions. This means that CPUE is not strictly an index of population in the discussion here, a limitation that turns out to be irrelevant for practical application of the model. Indeed, the model involves only catch and effort data, CPUE is never used directly. Notice, incidentally, that (1.12a) and (1.12d) are approximately the same for low levels of effort E_t.

1E. Recruitment Details

The final model assumption (1.13a) is essentially the recruitment function proposed by Deriso (1980); however, it is written here with somewhat different parameters to allow greater flexibility. Specific values of the parameter γ determine four cases of special interest:

(1.26) $\gamma = -\infty$: $R_t\{S\} = \alpha_t S$

(1.27) $\gamma = -1$: $R_t\{S\} = \alpha_t S/(1 + \beta S)$

(1.28) $\gamma = 0$: $R_t\{S\} = \alpha_t S\, e^{-\beta S}$

(1.29) $\gamma = 1$: $R_t\{S\} = \alpha_t S(1 - \beta S)$.

Each case above is either a valid mathematical limit for (1.13a) or simply the result of substituting the given value of γ. The first case (1.26) is a constant productivity model; α_t recruits are produced for each unit of stock biomass, regardless of stock size. The result (1.26) also follows from (1.13a) by setting $\beta = 0$. The next three cases (1.27)–(1.29) correspond to classical recruitment models, according to the following table:

Equation	Reference
(1.27)	Beverton and Holt 1957 (p. 49, equation 6.10)
(1.28)	Ricker 1954, 1958 (p. 238, equation 11.7)
(1.29)	Schaefer 1954 (bottom of p. 34)

Because of his slightly different expression for $R_t\{S\}$, Deriso (1980) noted the limiting versions (1.27)–(1.28), but he did not mention (1.29) as an additional possibility.

To complete the discussion of (1.13a), it is convenient to drop the subscripts:

$$(1.30) \quad R = \alpha S(1 - \beta\gamma S)^{1/\gamma}.$$

The parameters α and β should always be positive, although γ can have any sign. The curve (1.30) in the *SR* plane always passes through the origin (0, 0). When $\gamma > -1$, it has a maximum point (S_m, R_m) with coordinates (Appendix B)

$$(1.31) \quad \begin{aligned} S_m &= [\beta(1+\gamma)]^{-1} \\ R_m &= \alpha\beta^{-1}(1+\gamma)^{-(1+\gamma)/\gamma}. \end{aligned}$$

Furthermore, when $\gamma > 0$, the curve also has a second point S_0 (in addition to $S = 0$) where $R = 0$ (Appendix B):

$$(1.32) \quad S_0 = (\beta\gamma)^{-1}.$$

The coordinates (1.31)–(1.32) can be used as new parameters to rewrite (1.30) in the following two forms (Appendix B):

$$(1.33) \quad R = R_m(S/S_m)[1 + \gamma - \gamma(S/S_m)]^{1/\gamma}$$

$$(1.34) \quad R = (1+\gamma)^{(1+\gamma)/\gamma}\gamma^{-1}R_m(S/S_0)[(S_0 - S)/S_0]^{1/\gamma}.$$

Figures 2–4 represent recruitment curves for the three different formulations (1.30), (1.33), and (1.34), respectively, for various values of γ. Figure 2 includes all four cases (1.26)–(1.29); notice that the curves do not have a maximum for $\gamma < -1$. Figure 3 illustrates the role of the maximum for $\gamma > -1$ and shows that the intercept S_0 does not exist for $\gamma \leq 0$. Finally, Fig. 4 includes only curves with a maximum and two *R*-intercepts when $\gamma > 0$.

In Figure 3, the shape of the particular curve with $\gamma = -0.8$ suggests the mathematical fact that, as γ tends to -1 in (1.33), *R* takes the limiting form

$$(1.35) \quad R = R_m$$

for $S > 0$, that is, the constant recruitment model (1.13b). Thus, (1.13b) is really just another special case of (1.13a) when the latter is written in the form (1.33). Notice, however, that the limit (1.27) as γ tends to -1 with α and β fixed is different from the limit (1.35) as γ tends to -1 with S_m and R_m fixed.

From (1.31)–(1.32), it follows that

$$(1.36) \quad S_m = [\gamma/(1+\gamma)]S_0.$$

When $\gamma = 1$, the factor $\gamma/(1+\gamma)$ is 1/2, and the high point of the curve is midway between the intercepts at 0 and S_0. This fact corresponds to the symmetry of the Schaefer curve. In that context the quantity S_0 is called the "carrying capacity" (Schnute 1977), and the stock size S_m for optimum recruitment is well-known to be half the carrying capacity. To avoid this possibly unrealistic symmetry, Pella and Tomlinson (1969) added a parameter to the Schaefer model to produce a family of curves similar to that shown in Fig. 4. Here, the factor $\gamma/(1+\gamma)$ serves essentially the same purpose, as shown in (1.36).

The parameters α, β, and γ are given names in Table 1. The term "productivity parameter" for α comes from the limiting case (1.26), as well as the fact that (1.26) is an approximate version of (1.30) when *S* is small. Since the coordinates S_m and R_m of the optimal point (1.31) are both inversely proportional to β, this parameter is termed an "optimality parameter." Finally, γ is called a "recruitment limitation parameter" for its role in determining whether or not S_0 and R_m exist, that is, whether or not arbitrary stock and recruitment sizes are possible. The term "skewness parameter" would also be appropriate for γ, due to its significance in Fig. 4 and equation (1.36) above. The curve is symmetric when $\gamma = 1$, skewed left when $0 < \gamma < 1$, and skewed right when $\gamma > 1$.

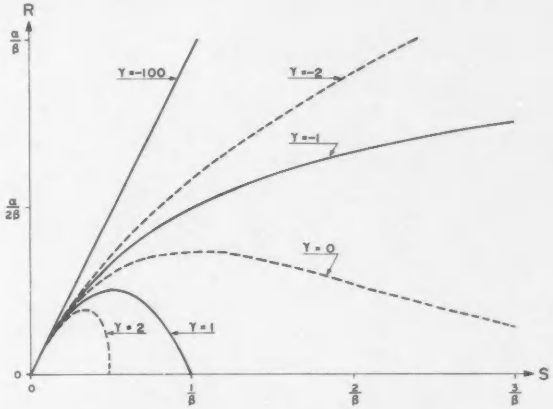

FIG. 2. Plot of recruitment *R* vs. stock *S* for six values of γ in equation (1.30) with fixed α and β. Cases of special interest include the models of Beverton and Holt ($\gamma = -1$), Ricker ($\gamma = 0$), and Schaefer ($\gamma = 1$). A large negative value of γ (e.g. $\gamma = -100$) gives essentially the constant productivity model $R = \alpha S$.

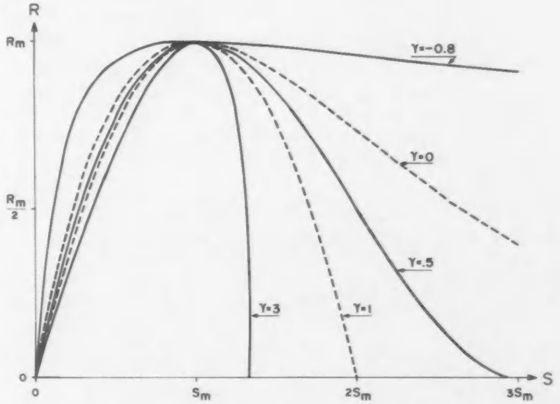

FIG. 3. Plot of recruitment *R* vs. stock *S* for five values of γ in equation (1.33) with a fixed maximum point (S_m, R_m). The models of Ricker ($\gamma = 0$) and Schaefer ($\gamma = 1$) are again special cases. As γ approaches -1 (e.g. $\gamma = -0.8$), *R* tends to the constant value R_m with a sudden jump from 0 at $S = 0$. When $\gamma > 0$, there is an intercept $S_0 > 0$ related to S_m by (1.36).

2. Difference Equations

The previous section completely describes an age structured model for a fish stock. It consists of the eight assumptions (1.6)–(1.13). These are quite general, although their main limitations are, first, that fishing and natural mortalities are

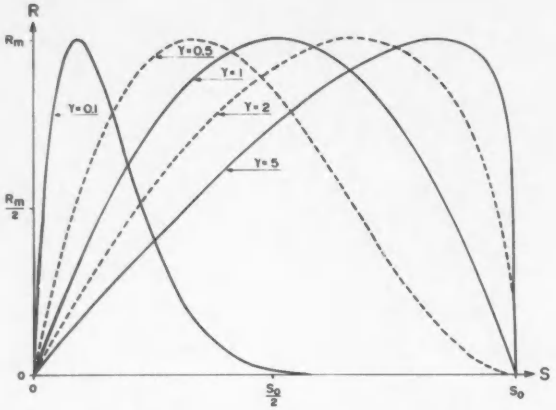

FIG. 4. Plot of recruitment R vs. stock S for five values of γ in equation (1.34) with fixed S_0 and R_m. The Schaefer case ($\gamma = 1$) is symmetric about $S_0/2$. Otherwise the curve is skewed left for $\gamma < 1$ and right for $\gamma > 1$.

presumed age-independent and, second, that recruitment to the fishery occurs at a distinct age k. To apply this model to total annual catch and effort data, it is necessary to derive equations that involve these data only. Such equations are called difference equations, because they typically involve changes, or differences, in functions of time t. In particular, this section proves mathematically and explains biologically the following eight consequences of the first five assumptions (1.6)–(1.10):

$$N_{a+1,t+1} - \tau_t N_{at} = 0 \tag{2.1}$$

$$N^*_{a+1,t+1} - \tau_t N^*_{at} = \rho\tau_t(N^*_{at} - \tau_{t-1}N^*_{a-1,t-1}) \tag{2.2}$$

$$N_{t+1} - \tau_t N_t - R_{t+1} = 0 \tag{2.3}$$

$$\begin{aligned} &N^*_{t+1} - \tau_t N^*_t - R^*_{t+1} \\ &\qquad = \rho\tau_t(N^*_t - \tau_{t-1}N^*_{t-1} - \upsilon_{t-k}R^*_t/V_{t-k}) \end{aligned} \tag{2.4}$$

$$N_t = C_t/(1 - \phi_t) \tag{2.5}$$

$$N^*_t = C^*_t/(1 - \phi_t) \tag{2.6}$$

$$\begin{aligned} N^*_{t+1} = {} & (1 + \rho)\tau_t N^*_t - \rho\tau_t\tau_{t-1}N^*_{t-1} \\ & + V_{t+1-k}R_{t+1}\{\phi_{t+1-k}N^*_{t+1-k}\} \\ & - \rho\tau_t\upsilon_{t-k}R_t\{\phi_{t-k}N^*_{t-k}\} \end{aligned} \tag{2.7}$$

$$\begin{aligned} &C^*_{t+1}/(1 - \phi_{t+1}) \\ &= (1 + \rho)\tau_t C^*_t/(1 - \phi_t) - \rho\tau_t\tau_{t-1}C^*_{t-1}/(1 - \phi_{t-1}) \\ &\quad + V_{t+1-k}R_{t+1}\{\phi_{t+1-k}C^*_{t+1-k}/(1 - \phi_{t+1-k})\} \\ &\quad - \rho\tau_t\upsilon_{t-k}R_t\{\phi_{t-k}C^*_{t-k}/(1 - \phi_{t-k})\}. \end{aligned} \tag{2.8}$$

Equation (2.1) is a minor variation of assumption (1.6). It can be regarded as a conservation statement; those fish at age a that survive year t are precisely the fish at age $a + 1$ that begin the next year $t + 1$. Similarly, (2.2) is a related conservation principle for biomass; however, the principle is not quite so simple because, due to growth, the weights w_{at} and $w_{a+1,t+1}$ are not the same. To prove (2.2), notice first from (1.6) that for $a \geqslant k + 1$

$$N_{a+1,t+1} = \tau_t N_{at} = \tau_t\tau_{t-1}N_{a-1,t-1}.$$

Subscripts of N in each of these three equal terms match the various subscripts of w in (1.9). Multiplying the above terms by their counterparts in (1.9) gives

$$N^*_{a+1,t+1} - \tau_t N^*_{at} = \rho(\tau_t N^*_{at} - \tau_t\tau_{t-1}N^*_{a-1,t-1}),$$

that is, (2.2). Notice that (2.2) and (1.9) are very similar mathematically, particularly when τ_t and τ_{t-1} are both 1. Biologically, (2.2) expresses conservation, not of biomass itself, but rather of biomass increments.

Equation (2.3) is similar to (2.1), except that (2.3) describes the entire population, rather than just one age class. Again, (2.3) is a conservation principle; the population in year $t + 1$ consists of survivors and recruits. To prove (2.3), sum (2.1) over ages a from k to ∞, and notice that

$$\sum_{a=k}^{\infty} N_{a+1,t+1} = \sum_{a=k+1}^{\infty} N_{a,t+1} = N_{t+1} - R_{t+1}.$$

This completes the proof of (2.3).

Just as (2.3) is the counterpart of (2.1) for the total population, (2.4) is the counterpart of (2.2) for the total biomass. Furthermore, the proof is similar. Since (2.2) is valid for $a \geqslant k + 1$, the proof begins by summing (2.2) over ages from $k + 1$ to ∞. Notice that

$$\begin{aligned} \sum_{a=k+1}^{\infty} N^*_{a+1,t+1} &= N^*_{t+1} - N^*_{k+1,t+1} - N^*_{k,t+1} \\ &= N^*_{t+1} - w_{k+1,t+1}\tau_t R_t - w_{k,t+1}R_{t+1} \end{aligned}$$

$$\sum_{a=k+1}^{\infty} N^*_{at} = N^*_t - w_{kt}R_t$$

$$\sum_{a=k+1}^{\infty} N^*_{a-1,t-1} = N^*_{t-1}.$$

Applying these three results to the sum of (2.2) and collecting terms gives

$$\begin{aligned} &N^*_{t+1} - \tau_t N^*_t - w_{k,t+1}R_{t+1} \\ &\quad = \rho\tau_t(N^*_t - \tau_{t-1}N^*_{t-1} - [w_{kt} + \rho^{-1}(w_{kt} - w_{k+1,t+1})]R_t). \end{aligned} \tag{2.9}$$

Here, the expression in square brackets reduces simply to $w_{k-1,t-1}$ as a result of the growth equation (1.9) when $a = k$. Consequently, (2.9) becomes (2.4), given the definitions (1.2) and (1.5) for R^*, υ, and V. This completes the proof of (2.4).

Like (2.2), (2.4) expresses conservation of biomass increments, in this case for the total population. Equation (2.4) is the counterpart of a similar equation in Deriso (1980, p. 269, equation 4), except that the earlier equation excludes the final term involving υ_{t-k} because Deriso's growth model (1.21) has the parameter $\upsilon_t = 0$ for every t. The new term gives (2.4) an interesting symmetry in the role of R^* on each side of the equation.

Equation (2.5) is a simple consequence of (1.7); it follows as usual on summing over ages a from k to ∞. Since ϕ_t represents survival, $1 - \phi_t$ refers to mortality. Thus, $C_t/(1 - \phi_t)$ might be called the "catch per unit mortality" (CPUM) in comparison with the more conventional catch per unit effort, CPUE. Even though CPUE may not index population in this model, (2.5) shows that the CPUM does. Similarly, (2.6) shows that the same concept applies to biomass. The straightforward proof is based on multiplying (1.7) by w_{at} and summing over ages a.

It follows from (2.6) that

$$N^*_t - C^*_t = \phi_t N^*_t;$$

consequently, from (1.2), (1.15), and (1.8):

$$R^*_t = V_{t-k}R_t\{\phi_{t-k}N^*_{t-k}\} \tag{2.10}$$

where it is understood that the function $R_t\{\cdot\}$ is specified by an assumption such as (1.13a) or (1.13b). By combining (2.4) and (2.10), one obtains (2.7), which is a recursion formula for calculating the biomass N_{t+1}^* at time $t + 1$ based on the biomass at two previous times t and $t - 1$. Furthermore, (2.6) allows one to convert (2.7) into (2.8), a similar recursion formula for the catch C_{t+1}^*. Even though (2.7) and (2.8) look rather complex, their biological meaning is identical to (2.4), that is, a conservation equation for biomass increments.

Equation (2.8) satisfies the criterion mentioned at the start of this section: it involves only the catch and effort data, C_t^* and E_t, for various years t. The dependence on C_t^* is shown explicitly, and E_t enters the equation through τ_t and ϕ_t via (1.10) and one of the formula pairs (1.11)–(1.12). Practical application of (2.8) involves making specific assumptions about the various parameters in the equation. For example, suppose that all parameters are independent of time and that survival and recruitment are given by (1.11a), (1.12a), and (1.13a). Then (2.8) becomes

$$\begin{aligned}(2.11)\qquad (1 - e^{-qE_{t+1}})^{-1}C_{t+1}^* &= (1 + \rho)e^{-M}(e^{qE_t} - 1)^{-1}C_t^* \\ &\quad - \rho e^{-2M-qE_t}(e^{qE_{t-1}} - 1)^{-1}C_{t-1}^* \\ &\quad + \alpha V(e^{qE_{t+1-k}} - 1)^{-1}C_{t+1-k}^* \\ &\qquad \times [1 - \beta\gamma(e^{qE_{t+1-k}} - 1)^{-1}C_{t+1-k}^*]^{1/\gamma} \\ &\quad - \rho\alpha v e^{-M-qE_t}(e^{qE_{t-k}} - 1)^{-1}C_{t-k}^* \\ &\qquad \times [1 - \beta\gamma(e^{qE_{t-k}} - 1)^{-1}C_{t-k}^*]^{1/\gamma}.\end{aligned}$$

Although (2.11) is rather complex, it can be regarded as a predictive equation for C_{t+1}^* based on the data

$$(2.12)\qquad C_{t-k}^*, C_{t+1-k}^*, C_{t-1}^*, C_t^*, E_{t-k}, E_{t+1-k}, E_{t-1}, E_t, E_{t+1}$$

and the seven parameters

$$(2.13)\qquad M, q, \rho, \alpha v, \alpha V, \beta, \gamma$$

where the eighth parameter k is presumed known. (Here, α, v, and V are confounded because these parameters occur only in the products αv and αV.) In principle, then, (2.11) could be used to estimate the parameters (2.13) by, say, nonlinear regression.

For many data sets, the estimation problem suggested by (2.11)–(2.13) may not be completely solvable; also, there may be problems related to the type of statistical error in (2.11). However, this example illustrates a general method to construct a model for catch and effort data. The key equation is (2.8), termed the *catch equation* in the rest of this paper. This follows from the first five model assumptions (1.6)–(1.10). The modeller's initial task is to incorporate into the catch equation a set of additional assumptions appropriate to the fishery in question. These always concern the parameters that drive the model. For example, (2.11) is based on time-independent parameters, as well as the last three model assumptions (1.11a), (1.12a), and (1.13a). This is only one of a very large number of possibilities. Other models might be based on (1.11c)–(1.12c). Furthermore, the parameters might be allowed to depend on time; for example, survivals might be related to environmental observations. Some parameters, such as those associated with growth and mortality, might be known from survey data. Fishing mortality might be independent of effort, or, as in (1.13b), recruitment might be independent of stock biomass. The modeller must apply his or her knowledge of the fishery to tailor the model to the situation. The advantage of the method here is that it provides a single framework in which numerous models can be tried and compared easily with one another. Thus, the catch equation serves as a starting point for the iterative model-building of Box and Jenkins (1970); it specifies a useful *class* of fisheries models. The next section compiles some of the possibilities.

3. Special Cases

The model (1.6)–(1.13) involves three flexible biological components: mortality, growth, and recruitment. To obtain an orderly list of variations in the catch equation, it is necessary to define the alternatives available for each of these three components. In this section, consider the case of constant parameters discussed above in connection with (2.11). Table 3 lists some of the main ways in which the model can be specialized. There are two options for mortality, three for growth, and four for recruitment, with an additional set of four possible recruitment submodels. All these cases have been singled out because they fundamentally affect the number of time lags and parameters in the catch equation, as explained later. In the theory here, these assumptions serve to guide the biologist in identifying a tentative model, along the lines of "step 2" in Box and Jenkins' (1970) model-building strategy. The next few paragraphs describe in detail the options listed in Table 3.

Mortality

Model M1 is simply the general case (1.11a)–(1.12a) in which fishing occurs at the start of the year; the associated parameters are M and q. The alternatives (1.11b)–(1.12b) and (1.11c)–(1.12c) are not particularly important here, as they do not fundamentally affect the structure of the catch equation. A more significant alternative is M2, the assumption that fishing mortality is constant. This model would be valid in fisheries where effort is adjusted by fishermen or by regulation to take a fixed annual fraction of available stock. For example, effort might be held at a fixed level from year to year, regardless of stock size; or effort might increase in years of low stock, but with a corresponding loss of efficiency. The resulting version of (2.8),

$$\begin{aligned}(3.1)\qquad C_{t+1}^* &= (1 + \rho)\tau C_{t+1}^* - \rho\tau^2 C_{t-1}^* \\ &\quad + V(1 - \phi)R_{t+1}\{\phi C_{t+1-k}^*/(1 - \phi)\} \\ &\quad - \rho\tau v(1 - \phi)R_t\{\phi C_{t-k}^*/(1 - \phi)\},\end{aligned}$$

involves only the catch C^*, not the effort E_t. Here, ϕ and τ are used as the associated mortality parameters.

Growth

Model G1 is the general case (1.14), with parameters ρ, V, and v. Model G2 is Deriso's (1980) restriction (1.22) that the extrapolated prerecruitment weight v is 0; this leaves only the two parameters ρ and V. Model G3 is the case of constant weight

$$(3.2)\qquad v = V;$$

by (1.14), (3.2) implies that $w_{at} = V$ for all a and t. In this case the value of ρ is irrelevant in (1.14); furthermore, if

$$(3.3)\qquad \rho = 0,$$

then the difference equation (1.9) also implies constant weight. Thus, (3.2) and (3.3) are companion conditions; either implies constant weight for ages $a \geqslant k$. When (3.3) is true, the catch equation (2.8) assumes the much simpler form

$$\begin{aligned}(3.4)\qquad C_{t+1}^*/(1 - \phi_{t+1}) &= \tau_t C_t^*/(1 - \phi_t) \\ &\quad + VR_{t+1}\{\phi_{t+1-k}C_{t+1-k}^*/(1 - \phi_{t+1-k})\}.\end{aligned}$$

TABLE 3. Special cases of the general model, corresponding to particular assumptions on mortality, growth, and recruitment. Each case is assigned a label and a brief description. The model parameters for each case are also listed.

Label	Parameters	Defining assumptions	Description
		Mortality	
M1	M, q	(1.11a) and (1.12a)	General mortality model
M2	τ, ϕ	(1.11a) and ϕ = constant	Constant fishing mortality
		Growth	
G1	ρ, V, v	(1.14) with $v \neq V$	General growth model
G2	ρ, V	(1.14) with $v = 0$	Deriso's growth model
G3	V	(1.14) with $v = V$	Constant weight
		Recruitment	
R1	α, β, γ	(1.13a) with $k > 2$	General recruitment model
R2	α, β, γ	(1.13a) with $k = 2$	Two-year recruitment
R3	α, β, γ	(1.13a) with $k = 1$	One-year recruitment
R4	R	(1.13b)	Constant recruitment
		Recruitment submodels for i = 1, 2, or 3	
Ria	α, β	Model Ri with $\gamma = 1$	Schaefer recruitment
Rib	α, β	Model Ri with $\gamma = 0$	Ricker recruitment
Ric	α, β	Model Ri with $\gamma = -1$	Beverton–Holt recruitment
Rid	α	Model Ri with $\beta = 0$	Constant productivity

This equation can also be obtained another way. When the weight w_{at} is constant, there is no essential mathematical distinction between N_t and N_t^*; these quantities differ only by the fixed factor V. Similar remarks apply to R_t^* and R_t. Consequently, the result (2.3) is valid with superscript asterisks on N and R; call this revised version (2.3*). Then (3.4) follows from (2.3*) exactly as the earlier equation (2.8) follows from (2.4). Notice that (2.3*) is much simpler than (2.4); (2.3*) is a first-order difference equation, while (2.4) is second order. Biologically, the assumption of constant weight allows conservation of biomass increment to be replaced by conservation of biomass itself. Indeed, (3.4) is just a biomass conservation equation.

The constant weight equation (3.4) has one other potential application. Suppose that recruitment depends on population numbers rather than biomass and that the catch data are in numbers rather than weight. Mathematically, one can represent this situation simply by letting $V = 1$ and dropping the superscript asterisks. Then (3.4) becomes

$$C_{t+1}/(1 - \phi_{t+1}) = \tau_t C_t/(1 - \phi_t) + R_{t+1} \tag{3.5}$$

which is the catch equation for C_t (as opposed to C^*) when recruitment depends on population numbers or, as in (1.13b), is independent of population variables.

Recruitment

The model R1 is simply the general recruitment model (1.13a) with parameters α, β, and γ. The case $k > 2$ (R1) is distinguished from $k = 2$ and $k = 1$ (R2 and R3, respectively) because the recruitment age k influences the lags appearing in the catch equation. Model R4 is the constant recruitment case (1.13b). As the discussion leading to (1.35) shows, this can also be considered a limiting form of (1.13a) with only one remaining parameter R. In this case the catch equation (2.8) reduces to

$$\begin{aligned} C^*_{t+1}/(1 - \phi_{t+1}) = {} & (1 + \rho)\tau_t C^*_t/(1 - \phi_t) \\ & - \rho\tau_t\tau_{t-1}C^*_{t-1}/(1 - \phi_{t-1}) + (V - \rho\tau_t)R. \end{aligned} \tag{3.6}$$

Finally, models R1, R2, and R3 all have submodels corresponding to special values of γ, as shown in Table 3. For example, R1a is Schaefer recruitment with $k > 2$, and R3b is Ricker recruitment with $k = 1$.

The two mortality models, three growth models, and four recruitment models give a total of $2 \times 3 \times 4 = 24$ possible variations to the catch equation. These are listed in Table 4, along with the corresponding model parameters and lags in catch and effort used to predict C^*_{t+1}. (For example, C^*_t has lag 1.) The full set of 24 possible equations need not all be listed here, but Table 5 shows all those obtained by combinations of (1) M1 or M2, (2) G1 or G3, and (3) R1 or R4. In general, the catch equation for a model follows from (2.8) or its counterpart (2.11) with constant parameters. The cases M2, G3, and R4 can be obtained from the specialized versions of the catch equation (3.1), (3.4), and (3.6), respectively.

It is convenient to devise a compact notation to refer to a model. Let "$\langle mgr \rangle$" refer to the combination of components Mm, Gg, and Rr. For example, ⟨111⟩ is the full model (2.11) with seven parameters (2.13). Similarly, ⟨214⟩ is the constant effort and recruitment model obtained by setting R_t constant in (3.1), or, equivalently, setting τ_t and ϕ_t constant in (3.6). Various historical models can, at least approximately, be represented in this notation as follows:

Model	Historical reference
⟨133a⟩	Schaefer 1957; Schnute 1977
⟨133⟩	Pella and Tomlinson 1969
⟨121⟩	Deriso 1980
⟨134⟩	Roff 1983

I will not give a detailed discussion of the approximations necessary to demonstrate the validity of the above table, except to comment briefly on Roff's (1983) model

$$C^*_{t+1} = A + BE_{t+1}C^*_t/E_t \tag{3.7}$$

with parameters A and B. Roff justified (3.7) with the ad hoc

TABLE 4. Models obtained by combining assumptions on mortality, growth, and recruitment. Labels are consistent with Table 3. Each model is listed with its associated catch lags, effort lags (if any), parameters, and parameter count.

Model, MGR	Lags		Parameters	
	Catch lags	Effort lags	Parameter list	Count
111	$1, 2, k, k+1$	$0, 1, 2, k, k+1$	$M, q, \rho, \alpha V, \alpha v, \beta, \gamma$	7
112	$1, 2, 3$	$0, 1, 2, 3$	$M, q, \rho, \alpha V, \alpha v, \beta, \gamma$	7
113	$1, 2$	$0, 1, 2$	$M, q, \rho, \alpha V, \alpha v, \beta, \gamma$	7
114	$1, 2$	$0, 1, 2$	M, q, ρ, RV, Rv	5
121	$1, 2, k$	$0, 1, 2, k$	$M, q, \rho, \alpha V, \beta, \gamma$	6
122	$1, 2$	$0, 1, 2$	$M, q, \rho, \alpha V, \beta, \gamma$	6
123	$1, 2$	$0, 1, 2$	$M, q, \rho, \alpha V, \beta, \gamma$	6
124	$1, 2$	$0, 1, 2$	M, q, ρ, RV	4
131	$1, k$	$0, 1, k$	$M, q, \alpha V, \beta, \gamma$	5
132	$1, 2$	$0, 1, 2$	$M, q, \alpha V, \beta, \gamma$	5
133	1	$0, 1$	$M, q, \alpha V, \beta, \gamma$	5
134	1	$0, 1$	M, q, RV	3
211	$1, 2, k, k+1$	—	$\tau, \rho, \phi\alpha V, \phi\alpha v, \phi\beta/(1-\phi), \gamma$	6
212	$1, 2, 3$	—	$\tau, \rho, \phi\alpha V, \phi\alpha v, \phi\beta/(1-\phi), \gamma$	6
213	$1, 2$	—	$\tau, \rho, \phi\alpha V, \phi\alpha v, \phi\beta/(1-\phi), \gamma$	6
214	$1, 2$	—	$\tau, \rho, (1-\phi)R(V-\rho\tau v)$	3
221	$1, 2, k$	—	$\tau, \rho, \phi\alpha V, \phi\beta/(1-\phi), \gamma$	5
222	$1, 2$	—	$\tau, \rho, \phi\alpha V, \phi\beta/(1-\phi), \gamma$	5
223	$1, 2$	—	$\tau, \rho, \phi\alpha V, \phi\beta/(1-\phi), \gamma$	5
224	$1, 2$	—	$\tau, \rho, (1-\phi)RV$	3
231	$1, k$	—	$\tau, \phi\alpha V, \phi\beta/(1-\phi), \gamma$	4
232	$1, 2$	—	$\tau, \phi\alpha V, \phi\beta/(1-\phi), \gamma$	4
233	1	—	$\tau, \phi\alpha V, \phi\beta/(1-\phi), \gamma$	4
234	1	—	$\tau, (1-\phi)RV$	2

TABLE 5. All possible catch equations for the combined mortality models M1 or M2, growth models G1 or G3, and recruitment models R1 or R4. Model numbers are labelled as the triple ⟨MGR⟩.

$$\begin{aligned}\langle 111\rangle \quad & (1-e^{-qE_{t+1}})^{-1}C^*_{t+1}\\ & = (1+\rho)e^{-M}(e^{qE_t}-1)^{-1}C^*_t - \rho e^{-2M-qE_t}(e^{qE_{t-1}}-1)^{-1}C^*_{t-1}\\ & \quad + \alpha V(e^{qE_{t+1-k}}-1)^{-1}C^*_{t+1-k}[1-\beta\gamma(e^{qE_{t+1-k}}-1)^{-1}C^*_{t+1-k}]^{1/\gamma}\\ & \quad - \rho\alpha v e^{-M-qE_t}(e^{qE_{t-k}}-1)^{-1}C^*_{t-k}[1-\beta\gamma(e^{qE_{t-k}}-1)^{-1}C^*_{t-k}]^{1/\gamma}\end{aligned}$$

$$\langle 114\rangle \quad \frac{C^*_{t+1}}{1-e^{-qE_{t+1}}} = \frac{(1+\rho)e^{-M}C^*_t}{e^{qE_t}-1} - \frac{\rho e^{-2M-qE_t}C^*_{t-1}}{e^{qE_{t-1}}-1} + RV - Rv\rho e^{-M-qE_t}$$

$$\begin{aligned}\langle 131\rangle \quad & (1-e^{-qE_{t+1}})^{-1}C^*_{t+1} = e^{-M}(e^{qE_t}-1)^{-1}C^*_t\\ & \qquad + \alpha V(e^{qE_{t+1-k}}-1)^{-1}C^*_{t+1-k}[1-\beta\gamma(e^{qE_{t+1-k}}-1)^{-1}C^*_{t+1-k}]^{1/\gamma}\end{aligned}$$

$$\langle 134\rangle \quad \frac{C^*_{t+1}}{1-e^{-qE_{t+1}}} = \frac{e^{-M}C^*_t}{e^{qE_t}-1} + RV$$

$$\begin{aligned}\langle 211\rangle \quad & C^*_{t+1} = (1+\rho)\tau C^*_t - \rho\tau^2 C^*_{t-1}\\ & \quad + \alpha V\phi C^*_{t+1-k}[1-\beta\gamma\phi(1-\phi)^{-1}C^*_{t+1-k}]^{1/\gamma}\\ & \quad - \rho\alpha v\tau\phi C^*_{t-k}[1-\beta\gamma\phi(1-\phi)^{-1}C^*_{t-k}]^{1/\gamma}\end{aligned}$$

$$\langle 214\rangle \quad C^*_{t+1} = (1+\rho)\tau C^*_t - \rho\tau^2 C^*_{t-1} + (1-\phi)RV - (1-\phi)\rho\tau Rv$$

$$\langle 231\rangle \quad C^*_{t+1} = \tau C^*_t + \alpha V\phi C^*_{t+1-k}[1-\beta\gamma\phi(1-\phi)^{-1}C^*_{t+1-k}]^{1/\gamma}$$

$$\langle 234\rangle \quad C^*_{t+1} = \tau C^*_t + (1-\phi)RV$$

assumption that CPUE should be roughly similar from one time step to the next. For comparison, see model ⟨134⟩ in Table 5. When qE_t is small for all t ($qE_t \ll 1$), then the catch equation for ⟨134⟩ takes the form

$$C^*_{t+1} = (qVR + e^{-M}C^*_t/E_t)E_{t+1}. \tag{3.8}$$

This is quite similar to Roff's model with the added advantage that (unlike Roff's) it predicts zero catch in year $t+1$ if there is no effort that year. Furthermore, (3.8) is based on three clearly stated hypotheses: (1) constant weight, (2) constant recruitment, and (3) low fishing mortality ($qE \ll 1$).

In any model ⟨*mgr*⟩, it is important to take note of the number of estimable parameters. As Table 4 indicates, this is not always the complete list of parameters for the separate model compo-

TABLE 6. A comparison of the Schaefer (R3a) and general (R3) recruitment models. The table lists estimable parameters for all models obtained by combining R3a with a mortality model (M1 or M2) and a growth model (G1, G2, or G3). The parameter count for this list is then compared with the corresponding parameter count from Table 4. Theoretically, the counts should differ by only one parameter, since R3a is obtained from R3 by setting $\gamma = 1$.

Model, MGR	Parameters	R3a	R3
113a	q, $(1+\rho)e^{-M} + \alpha V$, $\rho e^{-M}(e^{-M} + \alpha \upsilon)$, $\alpha V\beta$, $\rho\alpha\upsilon\beta$	5	7
123a	q, $(1+\rho)e^{-M} + \alpha V$, ρe^{-2M}, $\alpha V\beta$	4	6
133a	q, $e^{-M} + \alpha V$, $\alpha V\beta$	3	5
213a	$(1+\rho)\tau + \alpha V\phi$, $\alpha V\phi^2\beta/(1-\phi)$, $\rho\tau(\tau + \alpha\upsilon\phi)$, $\rho\tau\alpha\upsilon\phi^2\beta/(1-\phi)$	4	6
223a	$(1+\rho)\tau + \alpha V\phi$, $\alpha V\phi^2\beta/(1-\phi)$, $\rho\tau^2$	3	5
233a	$\tau + \alpha V\phi$, $\alpha V\phi^2\beta/(1-\phi)$	2	4

nents in Table 3. For example, the full model ⟨111⟩ theoretically involves eight parameters in Table 3: M, q, ρ, V, υ, α, β, and γ. However, Table 4 (and the earlier discussion of (2.11)–(2.13)) shows that the three parameters α, V, and υ are confounded, so that ⟨111⟩ involves only seven parameters. This is not surprising biologically. If only the catch biomass C_t is available, the model does not know if there are a large number of small fish or a smaller number of large fish. Consequently, the number recruited (proportional to α) is confounded with fish weight (proportional to V and υ). As the model becomes simpler, the list of estimable parameters becomes smaller. For example, ⟨234⟩ involves only two parameters: τ and $(1 - \phi)RV$. Again this is reasonable biologically. Since the model assumes constant fishing mortality, weight, and recruitment, it cannot distinguish among fishing survival $1 - \phi$, weight V, and recruitment numbers R; raising the value of one of these parameters can be compensated by lowering another.

It is often difficult to tell just by looking at a model precisely how many parameters are estimable. Although confounding is obvious in certain cases (such as those above) when parameters appear in products or sums, other cases involve more complex analytical expressions. Table 6 illustrates this difficulty by listing parameters for models with Schaefer recruitment at age $k = 1$ (model R3a). In this case, the model ⟨mg3a⟩ consistently involves two fewer parameters than ⟨mg3⟩, even though the submodel is obtained by restricting only one parameter, $\gamma = 1$. Thus, the apparent number of parameters in ⟨mg3⟩ may be wrong, at least for values of γ near 1. Mathematically, the problem occurs because, when $\gamma = 1$, a recruitment term and survival term combine. For example, the classical Schaefer model ⟨133a⟩ has the catch equation

$$(3.9)\qquad C^*_{t+1} = \frac{1 - e^{-qE_{t+1}}}{e^{qE_t} - 1}\left(e^{-M} + \alpha V - \frac{\alpha V\beta C^*_t}{e^{qE_t} - 1}\right) C^*_t$$

with the three parameters

$$(3.10)\qquad q,\ e^{-M} + \alpha V,\ \alpha V\beta.$$

Consistent with Schnute (1977), these correspond to a catchability, production rate, and carrying capacity, respectively. The production rate $e^{-M} + \alpha V$ results from the combination of survival (e^{-M}) and recruitment (αV).

The examples of Table 6 are not the only ones to be aware of. For instance, model ⟨134⟩ in Tables 4 and 5 apparently has three parameters, q, M, and RV. However, as shown above, the model takes the form (3.8) with only two parameters, M and qRV, when qE is small. Thus, the practitioner should anticipate problems with confounded parameters when attempting to find estimates from actual data. In real applications, some parameters are usually available independently and should not be estimated from catch and effort data. This is particularly true for the growth parameters ρ, V, and υ. A compelling advantage to the approach here is that it allows the modeller to build on prior biological knowledge.

4. Equilibrium

After estimating a model's parameters, the modeller often wishes to use them to determine an optimal harvest policy. Typically, the analysis begins by studying how the fishery would perform if all parameters remained fixed forever at their estimated values, along with a constant fishing effort E. The resulting situation is a theoretical equilibrium in which none of the model variables depend on time. This section describes equilibrium for model ⟨111⟩, which is the same as that for ⟨211⟩, since at equilibrium ϕ is constant:

$$(4.1)\qquad \phi = e^{-qE}.$$

The catch equation for model ⟨211⟩ in Table 5 becomes an equilibrium equation if catch C^* is presumed independent of the year t. Dropping the subscripts in this equation simplifies it considerably because the catch C^* can then be cancelled from all terms. One can then solve the simplified equation for C^* to obtain

$$(4.2)\qquad C^* = \frac{1-\phi}{\beta\gamma\phi}\left\{1 - \left[\frac{(1-\sigma\phi)(1-\rho\sigma\phi)}{\phi(\alpha V - \rho\alpha\upsilon\sigma\phi)}\right]^{\gamma}\right\}$$

where $\sigma = e^{-M}$ is a parameter independent of E. Thus, (4.2) describes equilibrium catch C^* as a function of equilibrium fishing survival ϕ and, by (4.1), implicitly as a function of E.

Although the function (4.2) is rather complex, it is possible to derive some of its main features. For example, notice that $C^* = 0$ when $\phi = 1$, that is, by (4.1), when $E = 0$. This, of course, simply means that no fishing gives no catch. It seems reasonable that some high level of effort E (and low survival ϕ) would also give $C^* = 0$, because the population would be driven to extinction. This turns out to be true, as illustrated in Fig. 5. There are three critical values of ϕ: a lower value ϕ_l where $C^* = 0$, a higher value ϕ_m where C^* takes a maximum value C^*_m, and a highest possible value $\phi = 1$ where $C^* = 0$ again. These conclusions, proved in Appendix C, are based on the following assumptions for the model parameters:

$$(4.3)\qquad 0 < \sigma < 1$$

$$(4.4)\qquad 0 < \rho < 1$$

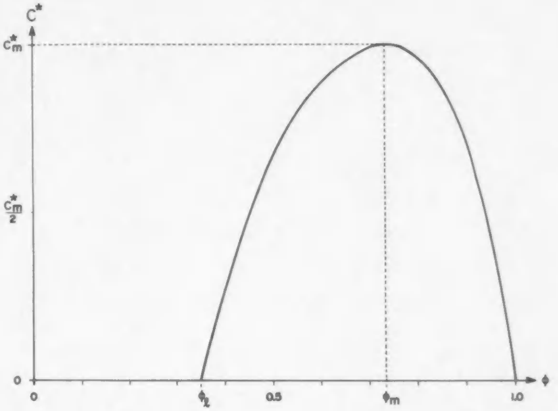

FIG. 5. Plot of equilibrium catch biomass C^* vs. fishing survival ϕ from equation (4.2). This figure, typical of the general case, is based on the parameters $\alpha = 0.8$, $\rho = 0.7$, $\upsilon = 0.5\,\text{kg}$, $V = 0.9\,\text{kg}$, $\alpha = 2.0$ fish/kg, and $\gamma = -1$ (i.e. Beverton–Holt recruitment). From (4.8) and (4.10) it turns out that $\phi_1 = 0.357$ and $\phi_m = 0.729$, respectively; also, $C_m^* = 1.157/\beta$.

$$(4.5) \qquad 0 < \upsilon < V$$

$$(4.6) \qquad 0 < \beta$$

$$(4.7) \qquad 1 < \alpha V + \sigma.$$

Conditions (4.3)–(4.6) are precisely the biological restrictions necessary to define σ, ρ, υ, V, and β in Section 1. The final condition (4.7) is required to guarantee that the combined effects of survival and recruitment are adequate to maintain the stock when there is no fishery.

An explicit formula for ϕ_l turns out to be (Appendix C)

$$(4.8) \qquad \phi_l = 2\{\sigma + \alpha V + \rho\sigma + [(\sigma + \alpha V - \rho\sigma)^2 + 4\rho\sigma(\alpha V - \alpha\upsilon)]^{1/2}\}^{-1}.$$

Notice in particular that ϕ_l does not depend on β or γ; biologically, this reflects the fact that extinction depends only on $R\{S\}$ for low values of S, where the approximation

$$R\{S\} \approx \alpha S$$

is valid regardless of β and γ. In fact, ϕ_l is determined by the four parameters

$$(4.9) \qquad \sigma, \rho, \alpha\upsilon, \alpha V.$$

Unfortunately, a formula like (4.8) for ϕ_m is not possible, in general; however, it can be shown (Appendix C) that ϕ_m satisfies

$$(4.10) \qquad \frac{\alpha\upsilon(1 - \rho\sigma\phi_m)^2 + (\alpha V - \alpha\upsilon)(1 - \rho\sigma^2{\phi_m}^2)}{(1 - \sigma\phi_m)(1 - \rho\sigma\phi_m)(\alpha V - \rho\sigma\alpha\upsilon\phi_m)} = \frac{1}{\gamma(1 - \phi_m)}\left\{\left[\frac{(\alpha V - \rho\sigma\alpha\upsilon\phi_m)\phi_m}{(1 - \sigma\phi_m)(1 - \rho\sigma\phi_m)}\right]^{\gamma} - 1\right\}.$$

This equation in ϕ_m must be solved numerically. A simple method for doing so was suggested by Schnute (1982, p. 48, section 8.5), although essentially the same method can be used to maximize C^* in (4.2) directly. Theoretical considerations (Appendix C) prove that (4.10) always has a solution ϕ_m between ϕ_l and 1, that is,

$$(4.11) \qquad \phi_l < \phi_m < 1.$$

The midpoint $(\phi_l + 1)/2$ of the interval (4.11) is a reasonable first guess for numerical iteration toward the solution ϕ_m of (4.10). Notice that ϕ_m depends on the four parameters (4.9), plus the fifth parameter γ. Once ϕ_m is found, the optimal effort and catch, E_m and C_m^*, can be calculated from (4.1) and (4.2), respectively.

Equations (4.2), (4.8), and (4.10) simplify greatly in the constant weight case, $\upsilon = V$; explicitly, they reduce, respectively, to

$$(4.12) \qquad C^* = \frac{1 - \phi}{\beta\gamma\phi}\left[1 - \left(\frac{1 - \sigma\phi}{\alpha V\phi}\right)^{\gamma}\right]$$

$$(4.13) \qquad \phi_l = 1/(\sigma + \alpha V)$$

$$(4.14) \qquad \frac{1 - \phi_m}{1 - \sigma\phi_m} = \frac{1}{\gamma}\left[\left(\frac{1 - \sigma\phi_m}{\alpha V\phi_m}\right)^{-\gamma} - 1\right].$$

Furthermore, for Schaefer recruitment with $\gamma = 1$, (4.14) can be solved explicitly. This, together with (4.1)–(4.2), gives

$$(4.15) \qquad \phi_m = 2/(1 + \alpha V + \sigma)$$

$$(4.16) \qquad C_m^* = (\sigma + \alpha V - 1)^2/(4\alpha V\beta)$$

$$(4.17) \qquad E_m = q^{-1}\log[(1 + \alpha V + \sigma)/2].$$

The expression (4.17) for E_m exhibits the biologically reasonable property that sustainable effort increases with increasing productivity αV and survival σ.

Incidentally, ϕ_m in (4.15) satisfies the condition

$$(4.18) \qquad \frac{1}{\phi_m} = \frac{1}{2}\left(\frac{1}{\phi_l} + \frac{1}{1}\right);$$

that is, ϕ_m is the harmonic mean (reciprocal average of reciprocals) of the end points of the interval (4.11). This condition is the counterpart of the traditional observation for the Schaefer model that the optimum is midway between extremes; that is, the apex of a parabola lies above the midpoint of the axis crossings. When $\gamma = 1$ in (4.12), C^* is a quadratic function of $1/\phi$.

5. Stochastic Models

The practical application of any model requires a method of estimating its parameters. This method, in turn, hinges on assumptions related to statistical error. The general model (1.6)–(1.13) is defined with time-varying parameters (Table 1) M_t, q_t, υ_t, V_t, and α_t, although these parameters are frequently presumed constant in later discussion. It is important, however, to show as in Section 2 that the main conclusions (2.1)–(2.8) are valid even with parameters dependent on time t, so that statistical variation can be introduced systematically. Explicitly, the model admits at least four possible sources of random behavior: (1) natural mortality M_t, or, equivalently, survival σ_t, (2) fishing efficiency q_t, or, equivalently, survival ϕ_t, (3) cohort weight υ_t and V_t, and (4) recruitment productivity α_t. Incidentally, item (2) in this list is also equivalent to a random error in measuring the effort E_t.

Just as there are many possible ways to specialize the deterministic aspects of the general model, so too are there many ways to specialize its stochastic aspects. In fact, the number of potential stochastic versions is so great that I make no attempt here to organize them as I have done for deterministic models in Section 3. The modeller must decide in a particular case where the most important sources of variation lie. The general plan is to extend the deterministic form of the model by adding error terms at appropriate places and then to estimate parameters by minimizing error. As the number of parameters increases, the apparent error can, of course, be reduced. More parameters give the model more flexibility, although, as explained below, this is not necessarily an advantage.

An extreme possibility is to include enough parameters so that the model equations can be fit exactly. This approach, called "stock reduction analysis" (SRA), was taken by Kimura and Tagart (1982) and Kimura et al. (1984). Essentially, they considered a model for catch data in which ϕ_t is an unknown parameter for every t. This gives a large number of equations with a large number of unknowns, and these can be solved numerically on a computer. Among other things, SRA gives fishing mortalities that precisely explain the catch data, in the spirit of "virtual population analysis" (VPA; Gulland 1955, Pope 1972) for catch at age data. Typically, SRA includes several more parameters than equations and involves locating those solutions that best correspond to the modeller's conception of the fishery.

One advantage of SRA is that it completely avoids the problem of statistical definition of the model. A disadvantage of any such method is that it will fail to locate trends in the data. Statistics is the science of data reduction, of locating a signal in the presence of noise. Without statistical assumptions, a model can only echo back the noise (errors) in the data. In the context of this paper, SRA is just one extreme in which the number of parameters becomes large. Indeed, a parameter estimation technique based on minimizing error will also work for SRA because one possibility is that the minimum error is precisely zero.

The first problem in introducing model error is to decide which of the various possible errors dominate. For example, consider the constant weight model ⟨131⟩ in Table 5. It has the form

$$(5.1) \qquad F_{t+1} = e^{-M}F_t + \alpha G_{t+1-k}$$

where, for convenience, we define

$$F_t = (1 - e^{-qE_t})^{-1}C_t^*$$

$$G_t = V(e^{qE_t} - 1)^{-1}C_t^*[1 - \beta\gamma(e^{qE_t} - 1)^{-1}C_t^*]^{1/\gamma}.$$

If we assume that survival e^{-M} and recruitment productivity α are both subject to multiplicative errors of about the same magnitude, then (5.1) could reasonably be written in the stochastic form

$$(5.2) \qquad \log(F_{t+1}) - \log(e^{-M}F_t + \alpha G_{t+1-k}) = \epsilon_t$$

where ϵ_t is normal with mean 0. Parameters might then be estimated by minimizing the sum of squares of errors ϵ_t in (5.2). Alternatively, one might hope to maximize the likelihood associated with (5.2), but an exact likelihood function is extremely difficult to calculate because (unlike classical autoregressive processes) the data C_t^* do not enter the model linearly.

The above idea seems temptingly appropriate to all models discussed in this paper. These typically have a left-hand side with data from year $t + 1$ and a right-hand side with data from earlier years. Let D_t represent either the difference between left-hand and right-hand sides or, as in (5.2), the difference of logarithms. The former choice is appropriate if the modeller believes that errors are additive, and the latter if errors are presumed multiplicative. Then, D_t is a function of observed data (represented as a vector X_t) and various parameters (represented as a vector θ). A general stochastic model, analogous to (5.2), is

$$(5.3) \qquad D_t(X_t, \theta) = \epsilon_t.$$

For example, in (5.2)

$$X_t = (C_{t+1-k}^*, C_t^*, C_{t+1}^*, E_{t+1-k}, E_t, E_{t+1})$$

$$\theta = (M, q, \alpha V, \beta, \gamma)$$

$$D_t = \log(F_{t+1}) - \log(e^{-M}F_t + \alpha G_{t+1-k}).$$

Although (5.3) seems reasonable, it may be inadequate for all situations. To see this, consider the general model ⟨111⟩, equation (2.11), obtained from (2.8) by assuming constant parameters. Notice that (2.8) involves both τ_t and τ_{t-1}, that is (from (1.25)), both M_t and M_{t-1}. Consequently, if we assume that variation in natural survival is important, the stochastic version of (2.11) should perhaps contain *two* independent errors ϵ_t and ϵ_{t-1} associated with years t and $t - 1$. This suggests replacing (5.3) with the more general stochastic model

$$(5.4) \qquad D_t(X_t, \theta) = \epsilon_t + \lambda\epsilon_{t-1}$$

where λ is a constant with

$$(5.5) \qquad -1 < \lambda < 1.$$

Theoretical reasons for the restriction (5.5) were given by Box and Jenkins (1970, p. 284, appendix A7.6).

The fundamental difference between (5.3) and (5.4) is that errors in (5.4) are correlated. In both models, the errors ϵ_t for various years t are presumed normal (with mean 0) and independent; however, the combined errors

$$\eta_t = \epsilon_t + \lambda\epsilon_{t-1}$$

in (5.4) are correlated. Explicitly,

$$\mathrm{corr}\,(\eta_t, \eta_{t-1}) = \lambda/(1 + \lambda^2).$$

In particular, (5.3) is the special case of (5.4) obtained when $\lambda = 0$. Parameters in (5.4), including λ, can be estimated by minimizing the sum of squares of errors

$$(5.6) \qquad S = \Sigma\,\epsilon_t^2$$

for the given data; however, ϵ_t is harder to compute in (5.4) than in (5.3). In addition, an unknown initial value of ϵ_t, say ϵ_0, is needed to start the process. Here is a recipe for calculating S in (5.6):

Step 1. Let a parameter vector θ be given, along with values of λ and ϵ_0. Also, let there be enough data to determine the required data vector X_t for $t = 1, \ldots, n$. For example, in (5.2) this would mean that C_t^* and E_t are known for $t = 2 - k$ and $t = 1, \ldots, n + 1$.

Step 2. Begin with $t = 1$.

Step 3. Compute ϵ_t from (5.4) as follows:

$$(5.7) \qquad \epsilon_t = D_t(X_t, \theta) - \lambda\epsilon_{t-1}.$$

Step 4. Replace t by $t + 1$, and repeat step 3. Continue until step 3 is completed with $t = n$.

Step 5. Compute S in (5.6) from $\epsilon_0, \epsilon_1, \ldots, \epsilon_n$. Notice that, since ϵ_t in (5.7) depends on θ and λ, S in (5.6) also depends on all these parameters, as well as the initial ϵ_0:

$$S = S(\theta, \lambda, \epsilon_0).$$

To minimize S as a function of its various parameters, one needs an algorithm that does not require explicit derivatives of S. The simplex method, as implemented by Schnute (1982), should perform well for the small number of parameters typically involved. Constraints, such as (4.3)–(4.6) and (5.5), may play a significant role. Schnute (1982, p. 47, section 8.4) gave an easy method for including such constraints. Also, certain parameters, such as the growth parameters ρ, υ, and V, may be known from studies external to the data. Schnute (1982, p. 43, section 8.2) described how to involve prescribed parameters easily. The minimum value of S may prove highly insensitive to the value of ϵ_0, and it may simply be best to prescribe $\epsilon_0 = 0$. In any case, both λ and ϵ_0 should be set equal to 0 as initial values for the search.

The stochastic model (5.4) is called a moving average (MA) model with lag 1 because the error is a combination (weighted average) of independent errors associated with time steps t and $t - 1$. The choice of lag 1 here is based on the biological arguments in the paragraph preceding (5.4); essentially, the general catch equation (2.8) is a second-order difference equation involving two time steps. To be consistent with this point of view, one might choose $\lambda = 0$ in a model based on the constant weight version (3.4), although there may always be some interest in seeing how efficiently the additional parameter λ removes error correlation. It is, in any case, important to base parameter estimates on a sum of squares of *uncorrelated* errors. Deriso (1980, p. 274) cited a comment by Box and Jenkins (1970, p. 213) that least squares estimates usually provide close approximations to maximum likelihood estimates. That is true, but the reader should note that Box and Jenkins (1970) referred not to the model errors (denoted η_t above), but their uncorrelated counterparts.

As suggested earlier, the possibilities for incorporating stochastic error into the deterministic models here are almost endless. In general, one could include a random influence anywhere in the difference equation and then solve for ϵ_0 to obtain an equation conceptually the same as (5.3) above. One could also include more lags in the moving average term on the right side of (5.4). Furthermore, there could be more than one source of error in catchability q_t with variable survival and recruitment. This would give rise to an errors-in-variables problem for which at least the relative magnitudes of errors would need to be known a priori. A full explication of all these possibilities is beyond the scope of this paper.

6. Model Identification

The technology developed here makes it possible to return with fresh insight to the question posed in the introduction: "Which model is right?" For example, we have seen that Roff's (1983) model (3.7) is essentially model ⟨134⟩ with constant weight and recruitment. Table 4 shows that ⟨134⟩ involves a minimal number of lags in the catch and effort data. Thus, Roff's model primarily raises the question: can we detect evidence of recruitment in our data? If so, then variations of the constant recruitment model (3.6), including Roff's, should be less effective than more general models which involve lag k recruitment terms. It may be that most fisheries have such noisy recruitment that no predictive values accrues from the lag k terms; the main information may come from lag 1 survival terms as Roff's example suggests. Whichever conclusion proves true in any particular case, the methods here make it possible to relate the model to biological reality. This is an important point because the model may have many purposes beyond simple prediction.

As described in the introduction, the process of iterating toward the best model (that is, model identification) has its roots in the general theory of time series analysis. Even there, the correct techniques are still a matter of current debate. For example, the recent paper by Tsay and Tiao (1984) rigorously develops a new method of ARMA model identification. If identification is difficult for linear ARMA models, it must be harder still for fisheries models with nonlinear recruitment. I doubt that a solid theoretical procedure is possible or even appropriate in this context, particularly since biological knowledge independent of catch and effort data can play a valuable role in the process.

This paper is devoted primarily to the first step of Box and Jenkins (1970) model building strategy: formulating an appropriate class of models. Once the modeller has a time series of catch and effort data, I think the next step is to accumulate all possible additional information, particularly growth parameters υ, V, and ρ and natural mortality M, if possible. To select a tentative model, consider the main apparent sources of error. For example, is recruitment primarily driven by the environment, as appears true for many shellfish? If so, then recruitment can perhaps best be modelled as a constant plus a stochastic term. Is effort measured reasonably well or are the effort data almost meaningless? In the latter case, it may be best to treat the fishing mortality as noise around a constant level.

In any application, it is important to consider the model's sensitivity to the parameters involved. For this reason, Section 3 includes frequent reference to possibilities for parameters that are confounded or drop out of the model in a special case. For instance, if β is small in the expression

$$\alpha S(1 - \beta\gamma S)^{1/\gamma},$$

then the value of γ may be irrelevant because the factor in parentheses is nearly 1. Also, if ρ is small in a second-order difference equation of the form

$$x_{t+1} - ax_t = \rho(x_t - bx_{t-1}),$$

then the equation collapses to first order and the parameter b may be inestimable, particularly when the error dominates the term on the right.

Bearing in mind numerous considerations, such as those mentioned in the two previous paragraphs, the modeller should be able to contrive a tentative model specifically tailored to the fishery in question. It will involve some parameters known a priori and others to be estimated from the data by minimizing a function such as S in (5.6). Attention now shifts to these estimates. How well determined are they? Can some parameters be dropped, thus simplifying the model, with no loss of predictive power? It is an element of folklore among most contemporary fisheries modellers that only two or three meaningful parameters can be estimated from any real catch-effort time series.

This paper is obviously only part of a potentially long discussion and debate, some of it already in the literature. In my view there is a need for many worked examples, which can be related to one another through a central theory, such as the one described here. If the community of researchers can agree on such a theory, then simulation studies can also play an important role in understanding the behavior of parameter estimates, particularly for the short time series (10–20 yr), which are all the data available in many fisheries. Significantly, Box and Jenkins (1970) included several sample data sets in their book, and these have since been used by numerous researchers to compare various methods with one another. Fisheries, likewise, could use such a carefully compiled benchmark, complete with a description of the known biology for each example. In short, much interesting work remains to be done. I believe progress will be most rapid if the various individual efforts can find a common focal point and thus be seen clearly as parts of a larger whole.

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I am very grateful for reviews of an earlier draft by R. Deriso and C. Walters. Their thoughtful comments led to substantial improvements in the final version. Furthermore, as I hope this paper makes clear, I share Walters' (1980) enthusiasm for Deriso's (1980) theoretical work. I would not have undertaken the development here without it. Finally, my thanks to M. Stocker for assistance in locating the herring data used for Fig. 1.

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Appendix A. Survival Calculations

To prove (1.24), notice that

$$\begin{aligned} N_{a+1,t+1} &= \tau_t N_{at} \text{ from (1.6)} \\ &= \tau_t (N_{at} - C_{at})/\phi_t \text{ from (1.7)} \\ &= \sigma_t (N_{at} - C_{at}) \text{ from (1.10).} \end{aligned}$$

The remainder of this appendix derives versions (a), (b), and (c) of the survival equations (1.11)–(1.12). It is sufficient to consider constant M, q, and E during just one year with time t from 0 to 1. For this discussion only, let P_t represent the cohort population at time t, and let Q_t represent the total catch of the cohort from time 0 to time t. We are interested primarily in P_0 and P_1, the initial and final populations, as well as the total catch Q_1 taken during year 0. Then, from (1.7) and (1.24)

$$\text{(A.1)} \qquad \phi_0 = (P_0 - Q_1)/P_0$$

$$\text{(A.2)} \qquad \sigma_0 = P_1/(P_0 - Q_1).$$

When fishing and natural mortality are concurrent, assume that the population P_t and the catch Q_t are governed by the differential equations

$$\text{(A.3)} \qquad dP/dt = -(M + qE)P$$

$$\text{(A.4)} \qquad dQ/dt = qEP.$$

It follows from (A.3) that

$$\text{(A.5)} \qquad P_t = e^{-(M+qE)t} P_0$$

and then from (A.4)–(A.5) that

$$\text{(A.6)} \qquad Q_t = [qE/(M + qE)][1 - e^{-(M+qE)t}]P_0.$$

Expressions for P_1 and Q_1 follow from (A.5) and (A.6). Substituting these into (A.1)–(A.2) gives (1.11b)–(1.12b).

If fishing occurs before natural mortality, then from (A.6) with $M = 0$, the total catch

$$\text{(A.7)} \qquad Q_1 = [1 - e^{-qE}]P_0$$

is removed first. This leaves a new initial population

$$P_0' = e^{-qE} P_0$$

to which (A.5) applies with $E = 0$; consequently,

$$\text{(A.8)} \qquad P_1 = e^{-M} e^{-qE} P_0.$$

Substituting (A.7)–(A.8) into (A.1)–(A.2) gives (1.11a)–(1.12a).

Finally, if natural mortality occurs first, then the number of surviving fish available to the fishery is

$$P_1'' = e^{-M}P_0$$

computed from (A.5) with $E = 0$. This gives the new initial population to which (A.6) applies with $M = 0$; consequently,

$$Q_1 = [1 - e^{-qE}]\, e^{-M}P_0. \tag{A.9}$$

Subtracting the catch Q_1 from the population P_1'' which survived natural mortality gives the same resulting value of P_1 as in (A.8) above. Substituting (A.8)–(A.9) into (A.1)–(A.2) gives (1.11c)–(1.12c).

Appendix B. Recruitment Parameters

The logarithmic derivative of the recruitment curve (1.30) is

$$\frac{1}{R}\frac{dR}{dS} = \frac{1 - (1+\gamma)\beta S}{S(1 - \beta\gamma S)}. \tag{B.1}$$

Consequently, $dR/dS = 0$ when $S = [(1+\gamma)\beta]^{-1}$; this is the expression for S_m in (1.31). Substituting that value of S into (1.30) also gives the expression for R_m in (1.31). Similarly, the value S_0 in (1.32) gives $R = 0$ in (1.30) for $\gamma > 0$.

The expressions (1.31) for S_m and R_m can be solved jointly for α and β with the results

$$\alpha = (R_m/S_m)(1+\gamma)^{(1/\gamma)} \tag{B.2}$$

$$\beta = [S_m(1+\gamma)]^{-1}. \tag{B.3}$$

Substituting (B.2)–(B.3) into (1.30) gives (1.33). Similarly, (1.36) follows from (1.31)–(1.32), and after substituting (1.36) into (1.33), one can obtain (1.34).

Appendix C. Equilibrium Calculations

The principal equation (4.2) follows from the catch equation ⟨211⟩ in Table 5 as described in Section 4. This expression for C^* vanishes when $\phi = 1$ or when

$$\phi(\alpha V - \rho\alpha v\sigma\phi) = (1 - \sigma\phi)(1 - \rho\sigma\phi). \tag{C.1}$$

Equation (C.1) is quadratic in ϕ; also, on dividing by ϕ^2, (C.1) is quadratic in $1/\phi$, and the roots turn out to be

$$1/\phi = [F \pm (G^2 + H)^{1/2}]/2 \tag{C.2}$$

where

$$F = \sigma + \alpha V + \rho\sigma$$

$$G = \sigma + \alpha V - \rho\sigma$$

$$H = 4\rho\sigma\alpha(V - v).$$

Since $\alpha > 0$, $1 > \sigma > 0$, $1 > \rho > 0$, and $V > v$, it follows that F, G, and H are all positive; furthermore,

$$\begin{aligned} F + (G^2 + H)^{1/2} &> F + G \\ &= 2(\sigma + \alpha V) \\ &> 2 \end{aligned}$$

since $\sigma + \alpha V > 1$ by hypothesis. Thus, choosing the "+" sign in (C.2) gives a value $1/\phi > 1$, i.e. $\phi < 1$. Similarly,

$$\begin{aligned} F - (G^2 + H)^{1/2} &< F - G \\ &= 2\rho\sigma \\ &< 2 \end{aligned}$$

so that the "−" sign in (C.2) gives $\phi > 1$. This shows that (C.1) has a unique root in the range $0 < \phi < 1$ corresponding to "+" in (C.2) and, consequently, proves the validity of the expression (4.8) for ϕ_l.

By Rolle's theorem (Clark 1972, p. 111), since $C^* = 0$ at ϕ_l and 1, there is a point ϕ_m between ϕ_l and 1 where

$$dC^*/d\phi = 0. \tag{C.3}$$

After considerable algebra, the condition (C.3) can be shown equivalent to (4.10). This calculation is facilitated by writing

$$C^* = K(1 - L^\gamma) \tag{C.4}$$

where the expressions K and L have definitions evident from (4.2). On taking the derivative of the logarithm of each side of (C.4), one can show that (C.3) is equivalent to

$$d(\log L)/d\phi = \gamma^{-1}(L^{-\gamma} - 1)\, d(\log K)/d\phi. \tag{C.5}$$

Condition (4.10) for ϕ_m follows from (C.5), after calculating the logarithmic derivatives of K and L.

How Do Bottlenose Dolphins, *Tursiops truncatus*, React to Oil Films under Different Light Conditions?

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In daylight, and again at night under a shading canopy, we observed the behavior of bottlenose dolphins (*Tursiops truncatus*) allowed to swim freely in a pool with three surface divisions, one of which contained either clear mineral oil, dark-tinted mineral oil, or a thin sheen of refined motor oil. Overall, they avoided oil both during the day and at night. The response broke down when we presented them with a thin sheen, especially at night; we suggest that such conditions represent the threshold for their ability to detect oil or their desire to avoid it. Irrespective of light conditions, the dolphins' tactile sense played a more important role than vision in perceiving, and ultimately avoiding, oil. The strength of their basic reaction dampens our fear that they might be unknowingly subjected to prolonged or repeated exposure to oil at sea.

De jour, puis de nuit sous un auvent assombrissant, les auteurs ont observé le comportement de dauphins à gros nez (*Tursiops truncatus*) nageant librement dans une piscine à trois diversions superficielles dont une contenait soit de l'huile minérale claire, de l'huile minérale foncée ou une mince couche d'huile à moteur raffinée. En général, les dauphins évitaient l'huile minérale pendant le jour et la nuit. Cette réaction disparaissait quand ils étaient en présence d'une mince couche d'huile, surtout la nuit. Les auteurs formulent l'hypothèse que de telles conditions représentent le seuil de leur capacité de détection de l'huile ou de leur désir de l'éviter. Indépendamment de la luminosité, le tact des dauphins jouait un rôle plus important que la vision dans la perception de l'huile et leur réaction pour l'éviter. Compte tenu de l'intensité de leur réaction fondamentale, on ne doit pas vraiment craindre qu'ils puissent être, à leur insu, exposés de façon prolongée ou répétée à des hydrocarbures en mer.

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Bottlenose dolphins (*Tursiops truncatus*) can detect (Geraci et al. 1983) and will avoid (Smith et al. 1983) oil on the surface of the water. This was determined by observing the reaction of dolphins presented with a dark-colored, nontoxic oil slick confined to a portion of a seawater holding pen. Their response was unequivocal. They detected the oil and hesitated to swim beneath it. Their few contacts with the oil resulted in an overt startle response which set the pattern for subsequent avoidance.

At sea, dolphins might encounter a broad spectrum of crude and refined oils, most of them lighter in color and viscosity than the colored mineral oil used in the avoidance studies. In fact, those most harmful would tend to form thin sheens that are not readily apparent to dolphins (Geraci et al. 1983). How might dolphins react to these substances which represent the greatest risk, and how effectively would they be able to avoid them at night when visual acuity is minimized?

We sought to answer these questions by observing, in daylight, the behavior of dolphins allowed to swim freely in a pool with three surface divisions, one of which contained either colorless mineral oil or a thin sheen of refined motor oil. The study was then repeated at night, under a canopy that excluded 92% of moonlight and starlight. This series enabled us to establish their threshold for detecting and avoiding oil, and provided a basis to make a reasonable prediction of the risk of their contacting oil at sea.

Materials and Methods

Three subadult female bottlenose dolphins, designated A, B, and C, were maintained at the Institute for Delphinid Research, Grassy Key, FL. They were fed herring (*Clupea harengus*), and were in good health as judged by clinical assessment, hematology, and blood chemistry. The animals had been given a 4-mo recess following a series of oil avoidance trials (Smith et al. 1983). The study took place between April 1982 and June 1983, with a 3-mo intermission between the daylight and nighttime trials.

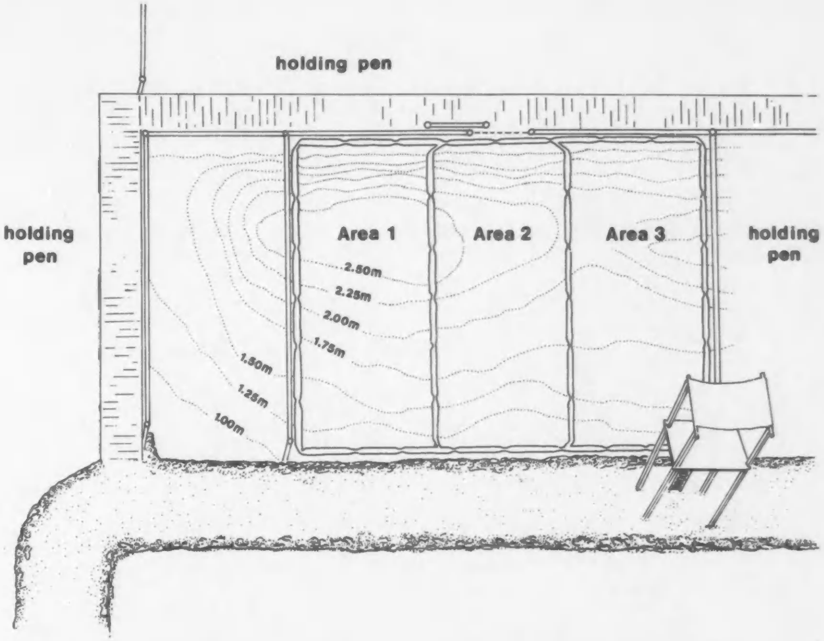

FIG. 1. Test pool used in oil-avoidance study, showing depth contours (at mean high tide), position of oil-confining booms, relationship to adjacent dolphin holding pens, and location of observation tower.

The study was conducted in a rectangular pen 14 × 11 m (154 m^2) formed by chain-link fence on three sides and on the fourth by a solid-filled causeway (Fig. 1). The pen was subdivided by oil-containment booms (Oil Containment Systems Corp., Cocoa, FL) into three areas measuring 4.5 × 11 m (50 m^2) with an average depth of approximately 1.75 m. The pen's configuration and dimensions were the same as in the previous study (Smith et al. 1983), but it was relocated 5 m toward deeper water to provide uniform depth. An access gate was located in area 2.

After the studies in daylight were completed, we covered the pen with a canopy of polypropylene shade fabric (Stuppy Inc., North Kansas, MO) designed to screen 92% of incoming light, in order to provide uniformly dark conditions. The material was supported by wooden framework which was 3.8 m high along the causeway side of the pen, and sloped down to 1.5 m above high water. Side panels of fabric extended down below the low tide level on the three sides of the pen bounded by chain-link fence (Fig. 2).

We tested the dolphins' reaction to each of three types of spills: clear slick, dark slick, and thin dark sheen. Slicks 1 cm thick were produced using 416 L of Primol 355 (Exxon Co., Houston, TX) mineral oil, either clear or colored with 0.75 $g \cdot L^{-1}$ artists' black oil paint (Liquitex Series 1147, Benney and Smith, Easton, PA). A thin sheen of 0.1 mm nominal thickness was produced by adding 6 L of Havoline SAE 30 motor oil (Texas Oil Co., New York, NY). The relative opacities of the three oil presentations were 0.7 for the dark oil and <0.05 for both the clear oil and the oil sheen, as measured by transillumination (Geraci et al. 1983).

Daytime Study

Two dolphins, A and C, were placed together in the study pen for a day to acclimate to the setting, before control sessions began. On each study day, one dolphin was put into the pen. A 45-min observation period began as soon as the animal entered, and three other 45-min observation periods were conducted at irregular intervals during the next 6–9 h. At the end of the day, the dolphin was returned to a holding pen where it was fed in the company of other *Tursiops*. Table 1 shows the testing protocol. Four oil-free control presentations were interspersed among the tests. Dolphins were never placed in the study pen on consecutive days. Rather, they were given 1–8 d of rest between oil-free sessions and 1–4 d between test sessions with oil.

We made video and audio recordings of each observation period, which included an account of the dolphin's underwater movements, its behavior, and the area in which it surfaced. Observed movements underwater were translated into an occupation frequency by counting each new area the dolphin entered after it submerged. We did not count the area in which it dove unless it resurfaced there, or left the area and reentered it. An area was counted only once on any single dive. We did not consider the amount of time an animal occupied a given area.

Nighttime Study

With the canopy in place at night, there was insufficient light to activate a conventional light meter. To measure visibility during each test, we adopted the following system. Black numbers 20 cm high and 2 cm wide were painted onto 30-cm^2 white posterboard. Ten individual cards each bore a different number between 0 and 9. Twice during each night's session, cards randomly selected by an individual stationed at one end of the study pool were held in the view of an observer at the opposite end. The individual holding the card moved toward the observer until the card could be read. The distance between card and observer was recorded for each trial.

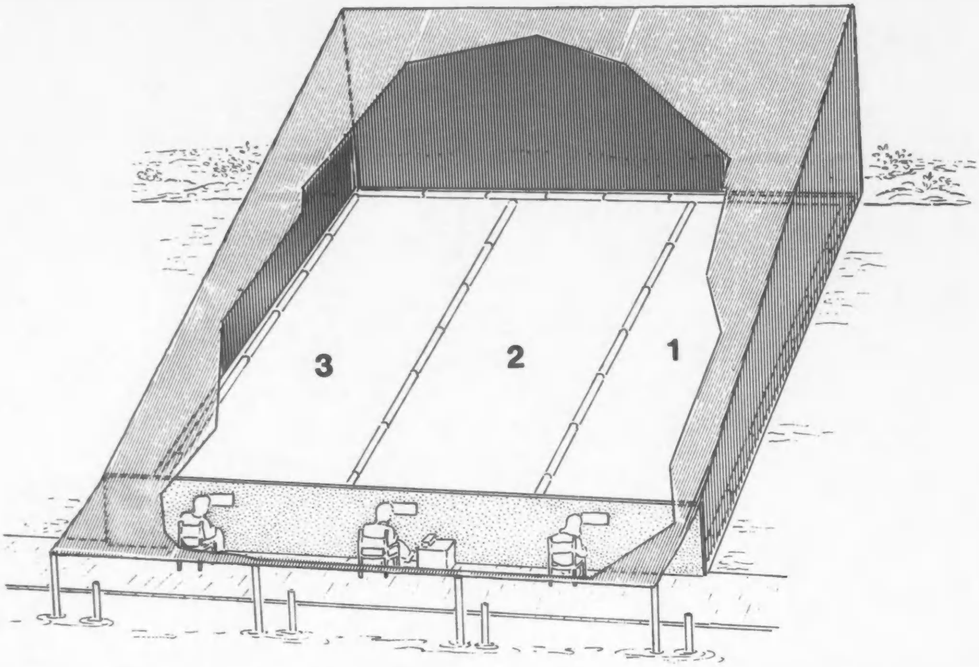

FIG. 2. For nighttime studies, the test pool was covered with a shade canopy to minimize moonlight and starlight. Numbered areas correspond to those in Fig. 1.

TABLE 1. Schedule of daytime oil-avoidance tests for each of two bottlenose dolphins from April to September 1982.

Presentation	No. of sessions[a]	Oiled area	Dates
Oil-free	3	—	Apr. 20 – May 3
Clear oil	3	2	May 7 – June 8
Oil-free	4	—	July 7–20
Sheen	4	3	July 24 – Aug. 3
Oil-free	4	—	Aug. 5–24
Dark oil	4	3	Aug. 27 – Sept. 3
Oil-free	2, 4[b]	—	Sept. 10–17

[a] Each session consisted of four 45-min observation periods.
[b] Dolphin A had two sessions and dolphin C had four.

TABLE 2. Schedule of nighttime oil-avoidance tests for each of three bottlenose dolphins from December 1982 to May 1983.

Presentation	No. of sessions[a]	Dates
Oil-free (daytime control)	7[b]	Dec. 3 – Feb. 14
Oil-free	4	Feb. 25 – Mar. 14
Dark oil	2	Mar. 18–24
Oil-free	1[c]	Mar. 31 – Apr. 6
Clear oil	2	Apr. 7–15
Oil-free	2	Apr. 20–27
Oil sheen	2	Apr. 28 – May 5

[a] Each session consisted of four 45-min observation periods.
[b] Dolphin A had six sessions.
[c] Dolphin C had two sessions.

Observations were carried out by three individuals, stationed in blinds at the end of each area (Fig. 2). The observer noted surfacings in the respective area, and comments were stored simultaneously on one channel of a stereo tape recorder; a hydrophone (Model ITC-6050C, Int. Transducer Corp., Goleta, CA 93117) was connected to the second channel to monitor underwater vocalizations. All three dolphins were tested in this phase of the study. For each session, a dolphin was placed in the pen alone. A 45-min observation period began as soon as the animal entered the pen; three similar observation periods were carried out over the next 4–5 h of the session.

The sequence and number of presentations of each test substance are shown on Table 2. We determined the dolphins' reaction to the canopy in a series of daytime control sessions. Once they acclimated to the new setting, nighttime studies began. Oil-free controls were interspersed among the oil-test presentations. The clear oil and oil sheen studies had few control sessions, since the animals' behavior was the same as had been established during the controls for the dark oil presentation. The location of the test oil differed for each dolphin, based on its individual preference shown during the control sessions.

Analysis of Data

For each oil-free and oil-test presentation, we ranked the three areas of the pen according to each dolphin's preference for surfacing and, for the daytime study, underwater occupation. Movements and preference for surfacing location were tested for significance using a Friedman two-way analysis of variance (Siegel 1956). Using Student's *t*-test, we compared each

TABLE 3. Daytime surfacing behavior of two bottlenose dolphins in a pen area before and after oiling.

		Dolphin A				Dolphin C			
	No. of observation periods[a]	No. of surfacings		% surfacings[b]		No. of surfacings		% surfacings[b]	
Study		Oil-free	Oiled	Oil-free	Oiled	Oil-free	Oiled	Oil-free	Oiled
Clear oil	12	629	4	34±10	<0.1±0.2[c]	289	2	15±7	<0.1±0.2[c]
Oil sheen	16	872	318	44±9	16±11[c]	1003	372	48±11	16±17[c]
Colored oil	16	695	0	34±10	0[c]	635	0	29±13	0[c]

[a] Number of 45-min observation periods during each of oil-free and oil presentations.
[b] $\bar{x}$ ± SD for all observation periods.
[c] Calculated t value indicates significant ($p < 0.01$) difference from oil-free controls.

TABLE 4. Daytime underwater occupation by two bottlenose dolphins in a pen area before and after oiling.

		Dolphin A				Dolphin C			
	No. of observation periods[a]	No. of occupations		% occupations[b]		No. of occupations		% occupations[b]	
Study		Oil-free	Oiled	Oil-free	Oiled	Oil-free	Oiled	Oil-free	Oiled
Clear oil	12	1040	343	40±3	16±12[c]	755	619	28±6	24±6
Oil sheen	16	992	677	33±5	24±5[c]	1132	774	36±9	23±7[c]
Colored oil	16	896	479	28±6	18±5[c]	824	541	25±9	18±4[c]

[a] Number of 45-min observation periods during each of oil-free and oil presentations.
[b] $\bar{x}$ ± SD for all observation periods.
[c] Calculated t value indicates significant ($p < 0.01$) difference from oil-free controls.

dolphin's use of a given pen area before and after adding the test substances. For the daytime study, comparisons were also made among the four oil-free control series to determine changes in behavior associated with time and experience.

Results

Daytime Studies

Dolphins A and C were selected for this series of studies because of their rapid acclimation to the experimental setting. They showed no overt response to the oil-containment booms, which proved to be a distraction for dolphin B.

Clear oil

During the first series of controls, both dolphins A and C preferred area 3, surfacing there 44 and 81% of the time, respectively. We placed the oil in area 2 to maintain the protocol of our previous experiment (Smith et al. 1983).

Both dolphins contacted the clear oil within 5 min of their initial exposure. They reacted with a startle response, submerged immediately, and swam rapidly into a non-oiled area. Dolphin A contacted the oil three more times within 15 min; thereafter it remained in area 3 for the duration of the first day. It completely avoided surfacing in the oil on the second and third days. By the middle of the second day, it began to surface again in oil-free area 1, as it had during the control periods. Dolphin C made a single contact with the oil on the first day, surfaced in it once within the first minute of exposure on the second day, and made no subsequent contact on days 2 and 3. Table 3 summarizes their surfacing frequencies in area 2 during test and control presentations.

The extent of the dolphins' underwater movements is reflected by the occupation frequency for each area. Dolphin A's occupation of area 2 decreased significantly ($t = 6.77$, $p < 0.01$) from 40 ± 3% during the control sessions to 16 ± 12% when the oil was in place (Table 4). Its movements were particularly restricted during the first six test observation periods. Thereafter, it began to swim under the oil in area 2 to surface in oil-free areas 1 and 3. During the clear oil presentation, its total number of occurrences in all areas decreased by 28%, from 2567 to 1854, reflecting its virtual confinement to area 3. Dolphin C showed no significant ($t = 1.99$, $p > 0.05$) overall change in its underwater occupation of area 2 after the oil was introduced (Table 4), and the pattern of its movements was the same in each of the three oil-test days.

Oil sheen

During 4 d of oil-free controls prior to introducing the oil sheen, the dolphins showed a significant preference for area 3. We therefore placed the oil in this area. Under calm conditions, the oil produced a uniform sheen, but influenced by light winds, it tended to aggregate in patches, forming a discontinuous pattern.

Within 2 min of entering the pen, both dolphins emerged in the area containing the sheen. They showed no obvious response then or during most of the subsequent surfacings in the sheen area. Dolphin C did show some reaction during the second and third observation periods on the first day, when it repeatedly surfaced in the sheen, breached, swam rapidly across the entire width of the pen, and exhaled forcefully on surfacing. Thereafter the dolphin's behavior returned to normal.

Both dolphins significantly avoided the oil-containing area, reducing their surfacing frequency in area 3 to 16% from control levels of 44 and 48% for dolphins A and C, respectively (t = 7.61 for A and 6.08 for C, $p < 0.01$) (Table 3). However, there was no consistency in their response. The dolphins would surface in the oiled area 50–100 times in one 45-min session and not at all in another. There was no trend indicating either habituation or heightened avoidance.

When oil was present, the dolphins reduced their underwater occupation of area 3 (t = 4.92 for A and 4.55 for C, $p < 0.01$) (Table 4). Unlike their erratic surfacing behavior, the pattern of underwater movements was relatively consistent.

Colored oil

During control sessions, the dolphins showed no significant area preference in their surfacing behavior. We placed the colored oil slick in area 3 to facilitate comparisons with the results of the oil sheen study.

The dolphins completely avoided contact with the dark-colored oil throughout the entire observation period (Table 3). They also significantly reduced their underwater occupation of the oiled area (t = 5.28 for A and 3.04 for C, $p < 0.01$) (Table 4). Dolphin C demonstrated its awareness of the slick by avoiding area 3 altogether for the first 5 min. Thereafter, when passing under the oil, it often rolled on its side, apparently to view the slick.

Controls

The study concluded with a final series of oil-free control sessions. The surfacing patterns for both dolphins differed significantly from those observed in previous control sessions (Table 5). In general, there was a shift away from the area that had previously contained oil; the only exception was for dolphin C, which after the clear oil study, showed the same preference that it had before oil was introduced.

Nighttime Studies

Three dolphins were used in this series of studies. During control sessions, dolphin B showed none of the undesirable behaviors previously displayed, and could therefore be included in the study.

Measurement of ambient light using the display card technique proved to be reliable and reproducible among the three observers. Visibility ranged between 3 and 14 m. Ambient light within this range did not, in itself, influence surfacing frequency and location.

Controls

With the structure in place during daylight hours and with no oil in the pen, dolphins A and B showed a significant preference for surfacing in area 3; dolphin C preferred area 2 (χ^2 = 12.5, 30.0, and 41.9 for A, B, and C, $p < 0.01$). The average number of surfacings for each animal was 99 ± 18 for each of 84 observation periods.

Thick dark oil

During nighttime control sessions, all three dolphins maintained the surfacing pattern that they had shown during the day. The only differences were slight shifts away from area 1 for dolphin A and area 3 for dolphin C. The dolphins significantly reduced their surfacing frequency in all areas by 13–23% (t = 2.62, 4.74, and 3.14 for A, B, and C, $p < 0.01$) compared with daytime controls.

We placed a 1-cm-thick slick of colored mineral oil in area 2. Within 5 min of entering the study pen, dolphins B and C surfaced once in the oil. During the same period, dolphin A apparently contacted the oil, judging from a ripple at the surface, but did not emerge enough to take a breath. After contact, the dolphins quickly submerged, then surfaced in an unoiled area; their breathing was rapid and shallow. For the remainder of that night, and throughout the second night, dolphins A and C made no further contact with the oil, whereas dolphin B contacted it once again, 34 min after entering the pen on the second night. Surfacing data for area 2 before and after introduction of the oil are given in Table 6. In all, the dolphins had more surfacings during the oil sessions than the nighttime controls (t = 2.33 and 2.39 for A and C, $p < 0.05$; t = 4.85 for B, $p < 0.01$), but no more than they had during daytime controls.

TABLE 5. Surfacing preference by area during control sessions for each oil-avoidance study (*$p < 0.05$, **$p < 0.01$, ns = not significant).

Study	Area preference during controls[a]		Conditions in previous study
	Dolphin A	Dolphin C	
A	3 > 2 > 1*	3 > 2 > 1**	—
B	3 > 1 > 2**	3 > 2 > 1**	Thick clear oil in area 2
C	1 = 2 = 3 ns	1 = 2 = 3 ns	Oil sheen in area 3
D	1 > 2 > 3**	2 > 1 > 3*	Thick dark oil in area 3

[a] Significance of area preference tested using Friedman analysis of variance by ranks.

Dolphins A and B showed no apparent reluctance to swim under the oil between areas 1 and 3; they surfaced in area 1 more frequently than they had during the controls. By contrast, dolphin C occupied area 3 almost exclusively during the remaining sessions.

Thick clear oil

During the control period, dolphins A and B showed the same surfacing patterns they had established during the controls for the dark oil study. Therefore, control data were combined for these two studies. The behavior of dolphin C differed significantly compared with the previous control. Its preference shifted from area 2 to area 1, and a second series of control sessions was needed to confirm the newly established pattern. In summary, dolphins A and B began this study by surfacing immediately in area 2 which had previously contained dark oil, whereas dolphin C avoided the area for over 20 min, preferring now to occupy area 1.

Since all three dolphins showed different area preferences, we tested them in different settings. In sequence, we placed a 1-cm-thick slick of clear oil in area 3 for dolphins A and B, and then moved it to area 1 for dolphin C. All three dolphins clearly avoided the oil (Table 6). The only contacts noted were two by dolphin B at the end of the second night and one by dolphin C in the fourth observation period of the first night. The animals showed little overt reaction following the contact, and no change in surfacing behavior and frequency.

Oil sheen

During control sessions, dolphins A and B showed the same surfacing patterns as they had in all previous controls, preferring area 3. Dolphin C showed a preference for area 2, the same pattern that it had established in control sessions for the dark oil study. None of the animals avoided the area where the oil had been in the previous study.

Based on their individual preferences, we placed the oil sheen

TABLE 6. Surfacing behavior of three dolphins during nighttime oil-avoidance tests. Data are for the area of the study pen to which the oil was added ($^*p < 0.01$, $^{**}p < 0.05$).

Study	No. of observation periods		No. of surfacings (% of total ± SD)					
			Dolphin A		Dolphin B		Dolphin C	
	Oil-free	Oiled	Oil-free	Oiled	Oil-free	Oiled	Oil-free	Oiled
Dark oil	16	8	454 (33±11)	0 (0)*	375 (29±11)	2 (<0.1)*	891 (78±24)	1 (<0.1)*
Clear oil	4[a]	8	204 (55±7)	0 (0)*	305 (70±8)	2 (<0.1)*	484 (57±14)	1 (<0.1)*
Oil sheen	8	8	390 (46±12)	124 (17±10)*	548 (68±13)	441 (46±21)**	624 (70±11)	1 (<0.1)*

[a] $n = 8$ for dolphin C.

in area 3 for dolphins A and B and in area 2 for dolphin C. Three distinct responses to the sheen were apparent (Table 6). Dolphin C avoided surfacing in the sheen after contacting it only once within 5 min of the first session. Yet, judging from its frequent use of unoiled areas on either side of the pen, the animal showed no reluctance to swim under the oil. Dolphin A statistically avoided the sheen ($t = 5.22, p < 0.01$), but surfaced in it at least 124 times during the two study nights. Dolphin B showed the least response to the sheen, surfacing in it over 440 times. It maintained its preference for area 3, but significantly ($t = 2.43$, $p < 0.05$) reduced its surfacings there from 68 ± 13% during controls to 46 ± 21% after the sheen was added.

Discussion

We presented the dolphins with three different oils under two conditions of visibility. Overall, they avoided oil both during the day and at night. The response broke down when we presented them with a thin sheen, suggesting that we had found the threshold for their ability to detect oil or desire to avoid it. Visual and tactile cues were instrumental in the dolphins' detection of the oil, and memory of its location influenced their behavior, even after the oil was removed.

In daylight, the dolphins completely avoided dark-colored mineral oil throughout the 4-d presentation. The response was more convincing than we had observed with these dolphins under the same condition 8 mo previously (Smith et al. 1983). At night, however, all three dolphins contacted the dark oil within 5 min of entering the pen, suggesting that they could not readily detect it, and emphasizing the importance of visual cues in the initial detection process. Recognition of the presence of oil came after contact, which produced a startle response and reinforced their subsequent avoidance.

The clear oil study was designed to determine whether tactile properties alone were sufficient to elicit avoidance of a substance which the dolphins could not detect (Geraci et al. 1983). Their incursion into clear oil within only 5 min of exposure during the day indicates that they were less aware of its presence than they were of the dark oil, which differed only in color. After a few initial contacts followed by a startle response, they avoided the clear oil altogether. As with the dark oil at night, contact apparently sensitized them to the presence of the oil, and using either memory of its boundaries, or subtle visual and acoustic cues to detect it, they avoided it altogether. Again tactile stimulation seemed to be a predominant influence in their response to oil.

At night, the dolphins' immediate behavior toward clear oil was unexpected. They avoided it for several hours, yet under the same conditions, they had contacted the dark oil within 5 min. A possible explanation for this paradoxical behavior lies in the sequence in which the dolphins were tested. In the nighttime experiments, the animals had first been tested with dark oil, and after contacting it, may have detected subtle visual or acoustic properties of the oil which enabled them to avoid contacting it again. When next presented with clear oil, approximately 3 wk later, they recognized the cues and two of the dolphins avoided it for 4–8 h, while the third made no contact at all. Had the sequence of presentations been reversed, as it was in the daytime studies, we might have seen a different pattern. In this context, the colorant may have been irrelevant to the study; the principal cue was tactile recognition of the oil, after which the dolphins relied on other sensory clues to detect its bounds, and memory to effect their avoidance.

The dolphins' response to the sheen during the day was different than for either of the thick oil presentations. They entered the sheen area in less than 2 min and showed no startle reaction. They apparently could detect the sheen because over the next 4 d they significantly reduced the number of surfacings in that area. Yet, their response was erratic. The dolphins would surface there 50–100 times in one 45-min session, and not at all in another. This might be explained by unavoidable discontinuities in the sheen that allowed the dolphins to surface in the test area without actually contacting the oil. Moreover, the sheen may have presented a less aversive stimulus which the dolphins tolerated to some extent.

We established the limits of oil detection and avoidance for dolphins by presenting them with an oil sheen at night. This was the only presentation in which the dolphins' behavior was not consistent, ranging from complete avoidance to virtual indifference. The latter response was not influenced by breaks in the sheen, which was protected from the wind by the canopy. The sheen was continuous, and the dolphins' inconsistent response indicates that such conditions represent their threshold for avoiding oil.

The dolphins' ability to avoid the sheen at all raises a question as to the sensory mechanisms used to detect it. It is unlikely that chemoreception was involved. This sensory mode has not been completely defined in dolphins (Herman and Tavola 1980; Nachtigall and Hall 1985), particularly with respect to aromatic hydrocarbons. Moreover, we used a small volume of oil which lacked the short-chain volatile components needed to elicit chemosensation in other vertebrates (Hellstrom and Doving

1983). The sheen was probably undetectable acoustically (Geraci et al. 1983) and visually, since its optical density as measured by our transillumination technique (Geraci et al. 1983) was the same as that of clear oil. Although the sheen did not produce a strong tactile response, it presumably provided enough tactile stimulation to influence the dolphins' behavior. Thereafter, avoidance may simply have been a matter of the dolphins' familiarity with the boom configuration of the pen area containing the sheen.

Memory proved to be an important component of the dolphins' response to oil. During the daytime control sessions between each oil presentation, the animals tended to avoid the area where the oil had been in the previous study (Table 5). Dolphin C showed the same reaction at night. This response highlights our suggestion that the dolphins were cuing as much on the distinct boundaries established by the booms as on the oil itself. How would free-ranging cetaceans be influenced? Coastal species might well recognize the boundaries of a previously oil-fouled area, yet their dependence on the region for food and social interaction could override any reluctance to re-occupy it.

In our previous study (Smith et al. 1983), dark-colored oil had served as a barrier to dolphins' movements underwater, and we had suggested that this effect might diminish with time. In the daytime series of the present study, we tested the same animals using clear oil over a longer period of time. The movements of dolphin A were highly restricted until midway through the second day, when it began to swim readily between the oil-free areas separated by the slick. Clear oil posed no such impediment to the movements of dolphin C; the animal's underwater occupation of all three areas was identical in both control and oil-test situations.

The dark oil and oil sheen only slightly impeded the dolphins' underwater movements during the day, partly because the substances were placed at one end of the pen and not in the middle area where the clear oil had been. Nevertheless, both the sheen and dark oil caused them to restrict their movements during all sessions, with no trend suggesting habituation.

We could not chart the dolphins' underwater movements in the nighttime studies. However, two of the animals (A and B) showed no apparent reluctance to swim under dark oil as judged from their surfacing behavior in the oil-free areas on either side of the slick. Dolphin C restricted its movements when dark oil, but not the sheen, was present. It is difficult, therefore, to predict the circumstances in which an oil spill at night would represent a barrier to movement.

This series of studies shows that dolphins are able to detect and avoid a variety of oils both during the day and at night. To accomplish this, they rely predominantly on vision, and can apparently perceive subtle cues other than color in thick, transparent slicks. Irrespective of light conditions, the dolphins' tactile sense played the most important role in their response to oil. This sense would serve them well in any encounter with spills at sea, particularly for those substances that are noxious or irritating. The strength of their reaction serves to dampen the fears of repeated exposure to oil spills at sea. As close as the dolphins were to oil, their overwhelming response was to avoid it.

Acknowledgments

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Biochemical Genetic Stock Identification of Chum Salmon (*Oncorhynchus keta*) in Southern British Columbia

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Beacham, T. D., R. E. Withler, and A. P. Gould. 1985. Biochemical genetic stock identification of chum salmon (*Oncorhynchus keta*) in southern British Columbia. Can. J. Fish. Aquat. Sci. 42: 437–448.

We used electrophoresis to examine genetic variability of 33 chum salmon (*Oncorhynchus keta*) stocks in southern British Columbia and used differences in genotypic frequencies among these stocks for estimating stock compositions in a weekly fishery in upper Johnstone Strait. Seven polymorphic loci were used for stock identification. Chum salmon from the Fraser River, Bute and Toba inlets, Vancouver Island, and the southern Mainland had significantly different allelic frequencies, but there was also significant heterogeneity in allelic frequencies at some loci within each region. Allelic frequencies were generally stable over a 2-yr period in nine stocks for which consecutive annual sampling was conducted. There was no significant two-locus linkage disequilibrium for the chum salmon stocks surveyed. Cluster analysis indicated that Fraser River and Bute and Toba Inlet stocks were distinctive, but Vancouver Island and Mainland stocks were not. The timing and relative abundance of Fraser River chum salmon in upper Johnstone Strait as estimated by electrophoretic analysis was confirmed by an in-river test fishery in the Fraser River.

Les auteurs ont utilisé l'électrophorèse pour étudier la variabilité génétique chez 33 stocks de saumon kéta (*Oncorhynchus keta*) peuplant les eaux de la Colombie-Britannique méridionale. Les différences entre les fréquences génotypiques ont servi à l'estimation de la composition des stocks faisant l'objet d'une pêche hebdomadaire dans la partie supérieure du détroit de Johnstone. À cet effet, sept loci polymorphiques ont été utilisés. Le saumon kéta du fleuve Fraser, des inlets Bute et Toba, des eaux de l'île Vancouver et du sud de la province possédait des fréquences alléliques significativement différentes, mais les fréquences alléliques à certains loci présentaient une hétérogénéité significative dans chaque région. Les fréquences alléliques ont été généralement stables au cours d'une période de deux ans chez neuf stocks qui ont fait l'objet d'un échantillonnage annuel consécutif. Il n'y avait aucun déséquilibre significatif de la liaison entre deux loci chez les stocks étudiés. Une analyse typologique a révélé que les stocks du fleuve Fraser et des inlets Bute en Toba étaient distincts et que ceux de l'île Vancouver et du continent ne l'étaient pas. L'abondance relative et la présence du saumon kéta du fleuve Fraser dans la partie supérieure du détroit de Johnstone, déterminées par analyse électrophorétique, ont été confirmées par une pêche expérimentale dans le fleuve Fraser.

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Chum salmon (*Oncorhynchus keta*) stocks returning to spawn in rivers flowing into Johnstone Strait, Strait of Georgia, and the Fraser River approach their natal spawning grounds from the north through Queen Charlotte Strait and then through Johnstone Strait (Fig. 1). These stocks can be exploited in several net fisheries during their spawning migrations. They are considered for management as the largest unit stock in British Columbia (Beacham 1984a).

Exploitation in a mixed stock fishery inevitably leads to extinction of less productive stocks when the exploitation rate in the fishery is greater than the sustained stock productivity. The fishery in Johnstone Strait is the largest mixed stock fishery in British Columbia, and thus the potential for elimination of less productive stocks is great. Tagging studies conducted to determine stock timing and compositions in Johnstone Strait and Georgia Strait fisheries (Pritchard 1929, 1931; Chatwin 1953; Manzer 1954; Anderson and Beacham 1983) indicated that Fraser River chum salmon migrate through Johnstone Strait and Strait of Georgia at the same time as do stocks from other rivers in the area. Chum salmon fisheries in Johnstone Strait must necessarily be mixed stock fisheries given the overlap in migration timing among stocks (Anderson and Beacham 1983).

Chum salmon stocks on the east coast of Vancouver Island have been enhanced artificially, while those originating from other rivers, particularly the Fraser, have not been enhanced to the same degree. The potential exists for overexploiting chum salmon from the Fraser River, which is the largest single chum salmon production area in British Columbia. Effective management of chum salmon fisheries in Johnstone Strait and Strait of Georgia clearly requires reliable estimates of stock composition to be available on an in-season basis.

Although scale parameters have had only limited success for

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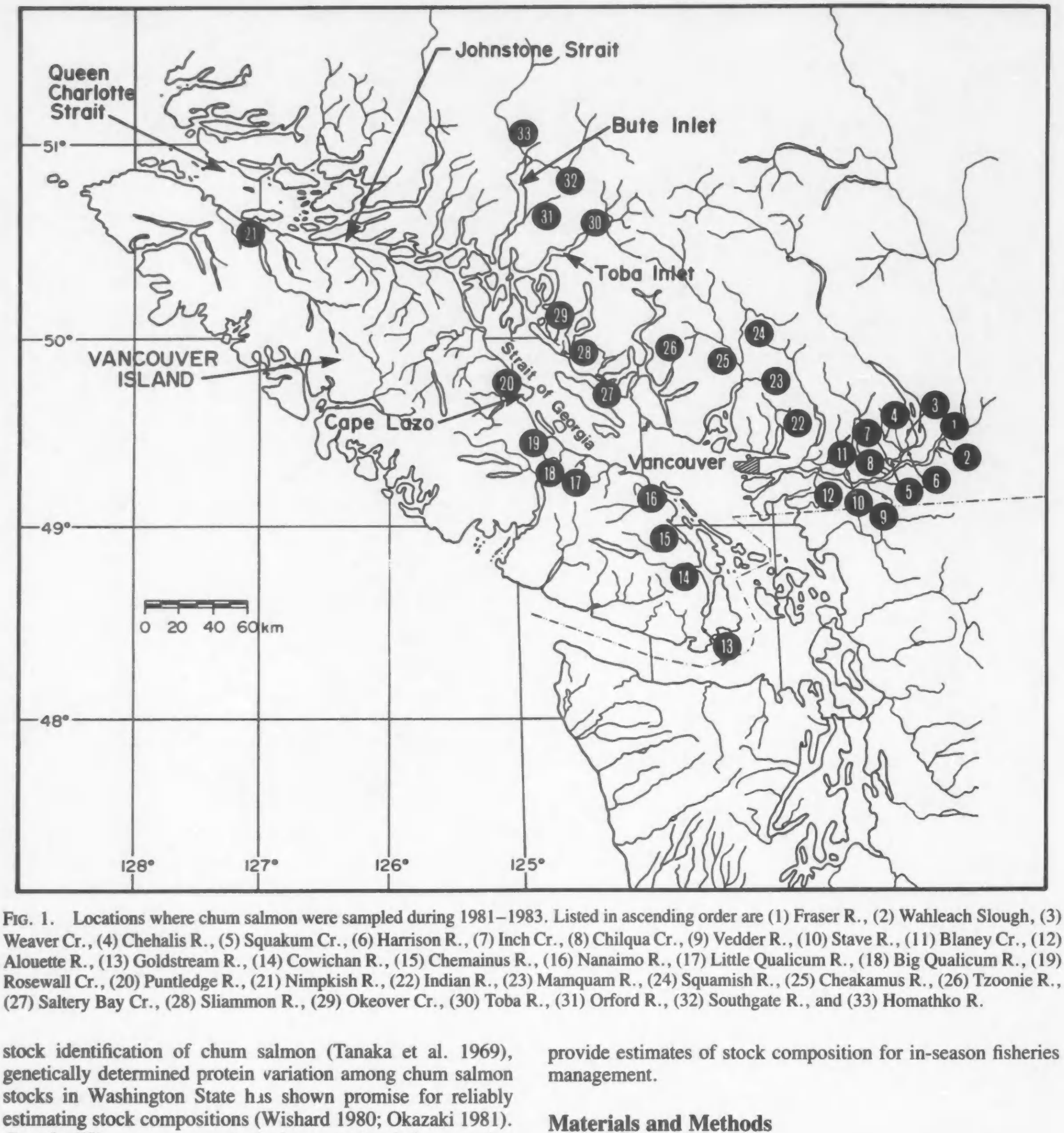

FIG. 1. Locations where chum salmon were sampled during 1981–1983. Listed in ascending order are (1) Fraser R., (2) Wahleach Slough, (3) Weaver Cr., (4) Chehalis R., (5) Squakum Cr., (6) Harrison R., (7) Inch Cr., (8) Chilqua Cr., (9) Vedder R., (10) Stave R., (11) Blaney Cr., (12) Alouette R., (13) Goldstream R., (14) Cowichan R., (15) Chemainus R., (16) Nanaimo R., (17) Little Qualicum R., (18) Big Qualicum R., (19) Rosewall Cr., (20) Puntledge R., (21) Nimpkish R., (22) Indian R., (23) Mamquam R., (24) Squamish R., (25) Cheakamus R., (26) Tzoonie R., (27) Saltery Bay Cr., (28) Sliammon R., (29) Okeover Cr., (30) Toba R., (31) Orford R., (32) Southgate R., and (33) Homathko R.

stock identification of chum salmon (Tanaka et al. 1969), genetically determined protein variation among chum salmon stocks in Washington State has shown promise for reliably estimating stock compositions (Wishard 1980; Okazaki 1981). Genetic differences among stocks have previously been used to provide estimates of stock compositions in sockeye salmon (*O. nerka*) (Grant et al. 1980) and chinook salmon (*O. tshawytscha*) fisheries (Miller et al. 1983). In 1981 we began spawning ground surveys of chum salmon stocks in southern British Columbia to examine variability among stocks in meristic and morphometric characters, as well as genetically based protein variation. Although meristic and morphometric characters showed initial promise for stock identification (Fournier et al. 1984), they were subsequently found to be unreliable (T. D. Beacham, unpubl. data). In the present study, we outline the results of our survey of protein variation in chum salmon, and illustrate that genetic differences among stocks may be used to provide estimates of stock composition for in-season fisheries management.

Materials and Methods

Chum salmon were sampled from 33 separate rivers tributary to Johnstone Strait, Strait of Georgia, and the Fraser River during 1981–83 (Fig. 1). The sampling techniques and locations sampled during 1981–82 were outlined by Beacham et al. (1983). Chum salmon on the spawning grounds were obtained with beach seines, pews, or by sampling fresh dead fish. Gill nets were set at the mouths of some rivers where access was difficult (Bute Inlet, Toba Inlet, Jervis Inlet). All chum salmon sampled during this study were mature adults.

Chum salmon were also sampled on a weekly basis for electrophoretic analysis during an 8-wk purse seine test fishery in upper Johnstone Strait from September 10, 1983, to October

25, 1983. Tissue samples were taken from 100 fish/wk, brought to the Pacific Biological Station, electrophoretic analyses conducted, and stock compositions estimated for use in formulation of management decisions the following week. In each week, samples were collected over a 3- to 5-d period, with approximately 20–35 fish sampled per day. Five or six sets were made per day from which the daily sample was obtained. A sample of chum salmon was also collected with gill nets on October 24, 1983, off Cape Lazo, Vancouver Island. Commercial fisheries for chum salmon had been conducted there during the preceding 2 wk. Chum salmon abundance in the Fraser River was determined by a gillnet test fishery, the details of which were outlined by Beacham and Starr (1982). This test fishery was conducted on a daily basis from October 4, 1983, to December 16, 1983.

During 1981, liver and muscle tissue samples were collected from all spawning chum salmon surveyed. During 1982 and 1983, heart, liver, and muscle tissue samples were collected from spawning adult chum salmon. All tissue samples were frozen and stored at −20°C for later electrophoretic analysis by a consultant. We verified the scoring of all gels from a complete photographic record. Horizontal starch gel electrophoresis, described by Utter et al. (1974), was used to detect protein variation. In 1981 we surveyed protein variation at 17 loci, but in 1982 and 1983, the survey of the monomorphic loci was discontinued. Three different loci were added in 1982 (*Agp-2*, *Lgg*, and *Pmi*), and the loci at which variants were detected, consistently resolved, and interpreted in a simple Mendelian manner are outlined in Table 1.

The designation of protein loci and alleles follows the system outlined by Allendorf and Utter (1979). If multiple loci code for a protein, the loci are numbered starting with the one which encodes the proteins with the least anodal migration. The most common allele at a locus was designated 100, and other alleles were assigned numbers according to the mobility of their homomeric protein products relative to that of the 100 allele. The interpretation of the banding pattern on the starch gels for all loci reported in this study (except *Me*) are outlined by Okazaki (1982). The genetic interpretation of observed variation at all loci was confirmed by the observation of Mendelian segregation of alleles in single family crosses (R. E. Withler, unpubl. data).

We determined allelic frequencies for each locus by summing the numbers of each allele and dividing by the total number of alleles counted. The frequency of genotypes at each locus for which variants were detected in each stock was tested for departures from Hardy–Weinberg equilibrium by chi-square. We used the likelihood-ratio statistic (*G*-test) (Sokal and Rohlf 1969) to test equality of allelic frequencies among and within geographic regions and between years for samples taken from the same stock. An approximate *F*-ratio (*G*-statistic summed over all loci/degrees of freedom) was used to test the relative magnitude of the sources of variation. We calculated genetic distance among stocks using Nei's (1978) statistic and the 10 loci indicated in Table 2, and constructed a dendogram from the matrix of the distances using the UPGMA method of Sneath and Sokal (1973). The Weaver Creek, Big Qualicum, Cheakamus, and Sliammon stocks were deleted because allelic frequencies for all 10 loci were not available.

TABLE 1. Enzymes and tissues used for investigation of protein variability in chum salmon. Buffers used were (1) an amine-citrate buffer described by Clayton and Tretiak (1972), (2) a Tris, citric acid, lithium hydroxide, and boric acid buffer described Ridgway et al. (1970), and (3) a Tris, boric acid, EDTA buffer described by Markert and Faulhaber (1965).

Enzyme	Tissue	Locus	Buffer
Alpha-glycerol-3-phosphate dehydrogenase (AGP, EC 1.1.1.8)	Muscle	*Agp-1*	1
	Heart	*Agp-2*	1
Isocitrate dehydrogenase (IDH, EC 1.1.1.42)	Muscle	*Idh-1*	1
	Liver	*Idh-3*	1
Malate dehydrogenase (MDH, EC 1.1.1.37)	Muscle	*Mdh-1,2*	1
	Muscle	*Mdh-3,4*	1
Malic enzyme (ME, EC 1.1.1.40)	Muscle	*Me*	1
Peptidase (leucylglycylglycine) (LGG)	Muscle	*Lgg*	2, 3
6-Phosphogluconate dehydrogenase (EC 1.1.1.44)	Muscle	*6-Pg*	1
Phosphomannoisomerase (PMI, EC 5.3.1.8)	Heart	*Pmi*	1, 3

We estimated stock compositions in the test fisheries by the method of Fournier et al. (1984). The results of previous electrophoretic screening of Fraser River, Vancouver Island, and Washington State chum salmon stocks (Wishard 1980) were incorporated into the baseline spawning ground samples. Based upon previous analysis of a 1981 test fishery off Big Qualicum, more reliable estimates of stock composition are obtained from genotypic rather than allelic frequencies (Fournier et al. 1984). The allelic frequencies for the stocks outlined by Wishard (1980) were converted to genotypic frequencies by assuming a Hardy–Weinberg genotypic distribution. Spawning ground samples for the Washington State stocks were pooled into those from Hood Canal, south Puget Sound, and north Puget Sound, as was done by Okazaki (1981). The British Columbia chum salmon stocks remained discrete in the baseline samples. Seven loci were used to estimate stock compositions: *Idh-1*, *Idh-3*, *Me*, *Pmi*, *Lgg*, *6-Pg*, and *Agp-2*. Estimates of the Fraser River, Bute and Toba Inlet, and other Canadian (Mainland plus Vancouver Island) and Washington State components were estimated by summing the contributions of the individual group members. We derived standard deviations of the estimates by bootstrap simulations. One hundred mixtures each containing 90% of the original mixture were constructed by randomly sampling the original mixture without replacement. Standard deviations of the estimates were derived from the 100 simulated samples. An index of abundance of each stock group in Johnstone Strait was determined by multiplying the weekly mean catch per set in the purse seine test fishery by the estimated proportion of each stock group in the weekly sample. Mean catch per unit effort in the Fraser River gillnet test fishery was determined as a 3-d running average.

We examined the accuracy of estimated stock compositions by constructing mixtures of known proportions of three groups of chum salmon and estimating stock compositions of these known mixtures using the seven loci previously noted. This was done for each comparison of Canadian non-Fraser (Vancouver Island and Bute and Toba inlets) stock versus other stocks, Washington State stock versus other stocks, and Fraser River stock versus other stocks. The known proportions examined ranged from 0 to 100% in 10% steps. The effect of mixture sample size on accuracy of estimated stock compositions was examined for mixtures of 50, 100, 150, 200, 250, 300, and 350 fish. Fifty mixtures were randomly constructed at each com-

TABLE 2. Observed allelic frequencies at polymorphic loci for 33 chum salmon stocks in southern British Columbia. Locations are illustrated that of the 100 allele.

			Idh-1		*Idh-3*					*Me*	
Stock	Year	*N*	100	60	100	25	40	85	110	100	125
Fraser River											
Fraser	1982	95	0.921	0.079	0.658	0.121	0.205	0.016	0.000	0.853	0.147
Wahleach	1982	100	0.920	0.080	0.605	0.065	0.270	0.060	0.000	0.874	0.126
Weaver	1981	100	0.920	0.080	0.632	0.074	0.289	0.005	0.000	0.845	0.155
Chehalis	1982	100	0.945	0.055	0.602	0.082	0.255	0.061	0.000	0.835	0.165
	1983	100	0.890	0.110	0.595	0.090	0.275	0.040	0.000	0.855	0.145
	Pooled	200	0.918	0.083	0.598	0.086	0.265	0.051	0.000	0.845	0.155
Squakum	1981	25	0.860	0.140	0.640	0.100	0.220	0.040	0.000	0.875	0.125
	1982	100	0.914	0.086	0.535	0.116	0.288	0.061	0.000	0.843	0.157
	Pooled	125	0.903	0.097	0.556	0.113	0.274	0.056	0.000	0.850	0.150
Harrison	1981	200	0.902	0.098	0.603	0.069	0.285	0.044	0.000	0.854	0.146
	1982	100	0.865	0.135	0.585	0.070	0.325	0.020	0.000	0.855	0.145
	Pooled	300	0.889	0.111	0.597	0.069	0.298	0.036	0.000	0.854	0.146
Inch	1981	100	0.867	0.133	0.660	0.016	0.309	0.016	0.000	0.870	0.130
	1982	53	0.896	0.104	0.558	0.058	0.317	0.067	0.000	0.849	0.151
	Pooled	153	0.881	0.119	0.623	0.031	0.312	0.034	0.000	0.862	0.138
Chilqua	1983	100	0.925	0.075	0.545	0.045	0.390	0.020	0.000	0.895	0.105
Vedder	1981	200	0.879	0.121	0.554	0.135	0.270	0.041	0.000	0.798	0.202
	1982	100	0.894	0.106	0.571	0.080	0.270	0.077	0.000	0.799	0.201
	Pooled	300	0.884	0.116	0.560	0.117	0.270	0.053	0.000	0.798	0.202
Stave	1982	100	0.923	0.077	0.585	0.045	0.320	0.050	0.000	0.791	0.209
Blaney	1982	100	0.883	0.117	0.515	0.075	0.310	0.100	0.000	0.880	0.120
Alouette	1983	100	0.945	0.055	0.583	0.100	0.275	0.042	0.000	0.935	0.065
Total		1773	0.904	0.096	0.587	0.081	0.288	0.044	0.000	0.854	0.146
Vancouver Island											
Goldstream	1982	92	0.908	0.092	0.592	0.076	0.304	0.027	0.000	0.647	0.353
Cowichan	1982	200	0.935	0.065	0.663	0.058	0.229	0.050	0.000	0.762	0.237
Chemainus	1981	53	0.915	0.085	0.509	0.066	0.396	0.028	0.000	0.821	0.179
	1982	100	0.945	0.055	0.495	0.090	0.380	0.035	0.000	0.885	0.115
	Pooled	153	0.935	0.065	0.500	0.082	0.386	0.033	0.000	0.863	0.137
Nanaimo	1981	100	0.895	0.105	0.610	0.030	0.305	0.050	0.005	0.810	0.190
	1982	100	0.924	0.076	0.565	0.070	0.295	0.070	0.000	0.758	0.242
	Pooled	200	0.910	0.090	0.587	0.050	0.300	0.060	0.002	0.784	0.216
Little	1981	200	0.940	0.060	0.632	0.045	0.265	0.045	0.013	0.743	0.257
Qualicum	1982	100	0.950	0.050	0.620	0.068	0.286	0.026	0.000	0.775	0.225
	Pooled	300	0.944	0.056	0.628	0.052	0.272	0.039	0.008	0.753	0.247
Big Qualicum	1981	200	0.957	0.043	0.635	0.043	0.305	0.018	0.000	0.796	0.204
Rosewall	1982	92	0.946	0.054	0.668	0.065	0.239	0.027	0.000	0.755	0.245
Puntledge	1981	200	0.926	0.074	0.587	0.085	0.272	0.054	0.003	0.780	0.220
	1982	100	0.960	0.040	0.640	0.086	0.242	0.032	0.000	0.705	0.295
	Pooled	300	0.938	0.063	0.604	0.085	0.262	0.047	0.002	0.756	0.244
Nimpkish	1982	87	0.891	0.109	0.500	0.175	0.256	0.069	0.000	0.879	0.121
Total		1624	0.934	0.066	0.606	0.068	0.281	0.042	0.002	0.783	0.217
Mainland											
Indian	1982	50	0.917	0.083	0.620	0.020	0.320	0.040	0.000	0.780	0.220
Mamquam	1982	101	0.960	0.040	0.604	0.045	0.307	0.045	0.000	0.780	0.220
Squamish	1983	100	0.930	0.070	0.605	0.056	0.296	0.043	0.000	0.775	0.225
Cheakamus	1981	100	0.940	0.060	0.709	0.015	0.219	0.056	0.000	0.830	0.170
Tzoonie	1982	107	0.933	0.067	0.589	0.084	0.266	0.061	0.000	0.769	0.231
Saltery Bay	1982	70	0.940	0.060	0.618	0.074	0.257	0.051	0.000	0.812	0.188
Sliammon	1981	100	0.951	0.049	0.593	0.057	0.284	0.067	0.000	0.780	0.220
Okeover	1982	103	0.932	0.068	0.545	0.099	0.317	0.040	0.000	0.807	0.193
Total		731	0.939	0.061	0.609	0.058	0.282	0.051	0.000	0.791	0.209
Bute and Toba inlets											
Toba	1983	103	0.961	0.039	0.680	0.034	0.248	0.039	0.000	0.816	0.184
Orford	1983	100	0.920	0.080	0.704	0.061	0.194	0.041	0.000	0.835	0.165
Southgate	1982	104	0.928	0.072	0.731	0.082	0.159	0.029	0.000	0.809	0.191
Homathko	1983	106	0.939	0.061	0.665	0.118	0.189	0.028	0.000	0.811	0.189
Total		413	0.949	0.051	0.690	0.074	0.197	0.039	0.000	0.817	0.183
Washington State[a]											
North Puget Sound			0.839	0.161	0.613	0.078	0.260	0.049	0.000	0.733	0.264
South Puget Sound			0.820	0.180	0.481	0.046	0.322	0.151	0.000	0.731	0.269
Hood Canal			0.718	0.282	0.575	0.064	0.254	0.107	0.000	0.723	0.277

[a] Derived from Wishard (1980).

in Fig. 1. The most common allele at a locus was designated 100, and other alleles were designated numbers according to the mobility relative to

Pmi		*Lgg*		*6-Pg*		*Agp-1*		*Agp-2*		*Mdh-1,2*		*Mdh-3,4*	
100	90	100	75	100	90	100	95	100	95	100	200	100	120
0.925	0.075	0.799	0.201	0.974	0.026	1.000	0.000	0.931	0.069	1.000	0.000	1.000	0.000
0.875	0.125	0.800	0.200	0.995	0.005	1.000	0.000	0.931	0.069	1.000	0.000	1.000	0.000
—	—	—	—	1.000	0.000	0.995	0.005	—	—	1.000	0.000	1.000	0.000
0.850	0.150	0.840	0.160	0.995	0.005	1.000	0.000	0.935	0.065	1.000	0.000	1.000	0.000
0.925	0.075	0.800	0.200	1.000	0.000	1.000	0.000	0.940	0.060	1.000	0.000	1.000	0.000
0.887	0.112	0.820	0.180	0.998	0.002	1.000	0.000	0.938	0.063	1.000	0.000	1.000	0.000
—	—	—	—	1.000	0.000	1.000	0.000	—	—	1.000	0.000	1.000	0.000
0.917	0.083	0.898	0.102	1.000	0.000	1.000	0.000	0.968	0.032	1.000	0.000	1.000	0.000
0.917	0.083	0.898	0.102	1.000	0.000	1.000	0.000	0.968	0.032	1.000	0.000	1.000	0.000
—	—	—	—	0.995	0.005	1.000	0.000	—	—	1.000	0.000	1.000	0.000
0.855	0.145	0.805	0.195	0.990	0.010	1.000	0.000	0.962	0.038	1.000	0.000	1.000	0.000
0.855	0.145	0.805	0.195	0.993	0.007	1.000	0.000	0.962	0.038	1.000	0.000	1.000	0.000
—	—	—	—	0.982	0.018	1.000	0.000	—	—	1.000	0.000	1.000	0.000
0.868	0.132	0.783	0.217	0.991	0.009	1.000	0.000	0.981	0.019	1.000	0.000	0.991	0.009
0.868	0.132	0.783	0.217	0.985	0.015	1.000	0.000	0.981	0.019	1.000	0.000	0.997	0.003
0.955	0.045	0.735	0.265	0.995	0.005	1.000	0.000	0.950	0.050	1.000	0.000	1.000	0.000
—	—	—	—	1.000	0.000	1.000	0.000	—	—	0.998	0.002	0.998	0.002
0.867	0.133	0.840	0.160	1.000	0.000	1.000	0.000	0.945	0.055	1.000	0.000	0.990	0.010
0.867	0.133	0.840	0.160	1.000	0.000	1.000	0.000	0.945	0.055	0.998	0.002	0.995	0.005
0.865	0.135	0.881	0.119	0.995	0.005	1.000	0.000	0.980	0.020	1.000	0.000	1.000	0.000
0.879	0.121	0.856	0.144	0.995	0.005	0.990	0.010	0.912	0.088	1.000	0.000	1.000	0.000
0.985	0.015	0.859	0.141	0.985	0.015	1.000	0.000	0.929	0.071	1.000	0.000	0.990	0.010
0.898	0.102	0.862	0.138	0.994	0.006	0.999	0.001	0.946	0.054	1.000	0.000	0.999	0.001
0.864	0.136	0.803	0.197	1.000	0.000	1.000	0.000	0.913	0.087	1.000	0.000	1.000	0.000
0.873	0.127	0.807	0.193	0.998	0.002	1.000	0.000	0.957	0.043	1.000	0.000	1.000	0.000
—	—	—	—	0.991	0.009	0.991	0.009	—	—	1.000	0.000	1.000	0.000
0.879	0.121	0.687	0.313	1.000	0.000	1.000	0.000	0.974	0.026	1.000	0.000	1.000	0.000
0.879	0.121	0.687	0.313	0.997	0.003	0.992	0.008	0.974	0.026	1.000	0.000	1.000	0.000
—	—	—	—	1.000	0.000	0.995	0.005	—	—	1.000	0.000	1.000	0.000
0.904	0.096	0.887	0.113	0.985	0.015	1.000	0.000	0.975	0.025	1.000	0.000	0.995	0.005
0.904	0.096	0.887	0.113	0.993	0.007	0.998	0.002	0.975	0.025	1.000	0.000	0.998	0.002
—	—	—	—	1.000	0.000	0.995	0.005	—	—	0.997	0.003	0.995	0.005
0.894	0.106	0.892	0.108	1.000	0.000	1.000	0.000	0.965	0.035	1.000	0.000	1.000	0.000
0.894	0.106	0.892	0.108	1.000	0.000	0.997	0.003	0.965	0.035	0.998	0.002	0.997	0.003
—	—	—	—	1.000	0.000	1.000	0.000	—	—	1.000	0.000	1.000	0.000
0.883	0.117	0.780	0.220	1.000	0.000	0.992	0.008	0.925	0.075	1.000	0.000	1.000	0.000
—	—	—	—	1.000	0.000	1.000	0.000	—	—	1.000	0.000	0.998	0.002
0.900	0.100	0.795	0.205	1.000	0.000	0.995	0.005	0.935	0.065	1.000	0.000	1.000	0.000
0.900	0.100	0.795	0.205	1.000	0.000	0.998	0.002	0.935	0.065	1.000	0.000	0.998	0.002
0.891	0.109	0.651	0.349	0.994	0.006	1.000	0.000	0.971	0.029	1.000	0.000	1.000	0.000
0.887	0.113	0.785	0.215	0.998	0.002	0.998	0.002	0.958	0.042	0.999	0.001	0.998	0.002
0.880	0.120	0.810	0.190	1.000	0.000	1.000	0.000	0.940	0.060	1.000	0.000	0.990	0.010
0.876	0.124	0.840	0.160	1.000	0.000	1.000	0.000	0.934	0.066	1.000	0.000	1.000	0.000
0.895	0.105	0.825	0.175	1.000	0.000	0.995	0.005	0.975	0.025	1.000	0.000	1.000	0.000
—	—	—	—	1.000	0.000	1.000	0.000	—	—	1.000	0.000	1.000	0.000
0.935	0.065	0.864	0.136	1.000	0.000	1.000	0.000	1.000	0.000	1.000	0.000	0.995	0.005
0.871	0.129	0.814	0.186	0.993	0.007	0.993	0.007	0.964	0.036	1.000	0.000	1.000	0.000
—	—	—	—	1.000	0.000	1.000	0.000	—	—	0.990	0.010	0.995	0.005
0.897	0.103	0.806	0.194	0.995	0.005	1.000	0.000	0.981	0.019	1.000	0.000	1.000	0.000
0.895	0.105	0.832	0.168	0.999	0.001	0.999	0.001	0.972	0.028	0.999	0.001	0.998	0.002
0.990	0.010	0.882	0.118	1.000	0.000	0.995	0.005	0.951	0.049	1.000	0.000	1.000	0.000
0.985	0.015	0.875	0.125	1.000	0.000	1.000	0.000	0.940	0.060	1.000	0.000	1.000	0.000
0.933	0.067	0.913	0.087	1.000	0.000	1.000	0.000	0.984	0.016	1.000	0.000	0.995	0.005
0.981	0.019	0.901	0.099	1.000	0.000	0.995	0.005	0.972	0.028	1.000	0.000	0.995	0.005
0.973	0.027	0.893	0.107	1.000	0.000	0.998	0.002	0.962	0.038	1.000	0.000	0.998	0.002
0.810	0.190	0.814	0.196	0.990	0.010	—	—	0.871	0.129	—	—	—	—
0.762	0.258	0.718	0.282	0.988	0.012	—	—	0.917	0.083	—	—	—	—
0.804	0.196	0.691	0.309	0.992	0.008	—	—	0.836	0.164	—	—	—	—

TABLE 3. Results of *G*-tests of heterogeneity of allelic frequencies among and within regions and between years surveyed for chum salmon stocks in southern British Columbia (*$P < 0.05$, **$P < 0.01$).

	Idh-1		*Idh-3*		*Me*		*Pmi*		*Lgg*		*6-Pg*		*Agp-1*		*Agp-2*		Total		
Source of variation	df	*G*	df	*G*	df	*G*	df	*G*	df	*G*	df	*G*	df	*G*	df	*G*	df	*G*	Standardized measure
Among regions	3	27.72**	9	39.00**	3	58.54**	3	39.43**	3	33.27**	3	16.99**	3	2.01	3	11.86**	30	228.82**	7.63
Within regions	29	36.90	87	224.19**	29	95.56**	25	69.70**	25	85.72**	29	43.65*	29	29.28	25	61.41**	278	646.41**	2.33
Fraser	11	15.49	33	93.77*	11	36.46*	10	47.00*	10	29.75	11	25.35**	11	13.31	10	19.05	107	280.18**	2.62
Bute–Toba	3	3.54	9	16.63	3	7.32	3	14.06*	3	4.70	3	0.00	3	2.72	3	5.58	30	54.55**	1.82
Vancouver Island	8	14.37	24	80.82**	8	47.96**	7	2.84	7	51.27**	8	12.45	8	7.39	7	16.18*	77	233.28**	3.03
Mainland	7	3.50	21	32.97*	7	3.82	5	5.80	5	3.07	7	5.85	7	5.86	5	20.60**	64	81.47	1.27
Between years	9	9.46	27	33.93	9	7.60	1	4.98*	1	0.83	9	1.60	9	0.19	1	0.00	66	58.59	0.89
Chehalis	1	3.35	3	1.08	1	0.17	1	4.98*	1	0.83	1	0.00	1	0.00	1	0.00	10	10.41	1.04
Squakum	1	0.74	3	1.89	1	0.11	—	—	—	—	1	0.00	1	0.00	—	—	7	2.74	0.39
Harrison	1	1.41	3	3.06	1	0.01	—	—	—	—	1	0.03	1	0.00	—	—	7	4.51	0.64
Inch	1	0.23	3	9.60*	1	0.10	—	—	—	—	1	0.00	1	0.00	—	—	7	9.93	1.42
Vedder	1	0.15	3	6.47	1	0.00	—	—	—	—	1	0.00	1	0.00	—	—	7	6.62	0.95
Chemainus	1	0.57	3	0.68	1	1.84	—	—	—	—	1	0.10	1	0.00	—	—	7	3.19	0.46
Nanaimo	1	0.71	3	4.03	1	1.32	—	—	—	—	1	1.47	1	0.00	—	—	7	7.53	1.08
Little Qualicum	1	0.08	3	4.49	1	0.60	—	—	—	—	1	0.00	1	0.07	—	—	7	5.24	0.75
Puntledge	1	2.22	3	2.63	1	3.45	—	—	—	—	1	0.00	1	0.12	—	—	7	8.42	1.20
Total	41	74.08**	123	297.12**	41	161.70**	29	114.11**	29	119.82**	41	62.24*	41	31.48	29	73.27**	374	933.82**	2.50

bination of sample size and known proportion. For example, 50 mixtures were constructed each of sample size 50 and having 10% Canadian non-Fraser chum salmon. The estimated stock composition of this mixture sample size and known stock proportion combination would be the mean of the 50 estimates derived from the 50 simulated samples. Then 50 new mixtures each of sample size 100 were constructed having 10% Canadian non-Fraser chum salmon, and the mean of the 50 estimates was determined. Thus, 350 (7 × 50) mixtures were constructed in our investigation of the accuracy of our estimates of 10% Canadian non-Fraser stocks. In our overall evaluation of our accuracy of our estimates of the Canadian non-Fraser stock, 3850 (350 × 11) mixtures were constructed and stock compositions determined. The same procedure was employed for Fraser River and Washington State stocks when we investigated the accuracy of the estimates of stock composition.

Results and Discussion

Population Structure

Allelic frequencies at seven loci differed among the regions outlined in Table 2. Of 216 comparisons of the observed genotypic frequencies with those expected under Hardy–Weinberg equilibrium, 14 (6%) deviated significantly. These 14 instances, distributed over six loci, were due to heterozygote deficiencies. Chum salmon from the Fraser River generally had a lower frequency of Idh-1^{100} than did chum salmon from the other areas (Tables 2, 3). They also had a higher frequency of Me^{100} than did chum salmon in the other regions. Chum salmon from Bute and Toba inlets had a higher frequency of Idh-3^{100} and Pmi^{100} than did chum salmon in the other areas (Tables 2, 3). Chum salmon from Vancouver Island had a lower frequency of Lgg^{100} than did other chum salmon.

Allelic frequencies at each locus were not always similar among stocks within a region. Only at *Idh-1* and *Agp-1* was there no heterogeneity within a region (Table 3). This analysis clearly indicates that there is restricted gene flow among stocks within a region. Nine stocks were sampled for two consecutive years. Of the 56 comparisons of homogeneity of allelic frequencies, only 2 were significant (Table 3). This stability of allelic frequencies between years eliminated the necessity of annual sampling for each stock in order to determine allelic frequencies for baseline data.

Allelic frequencies for all loci listed in Table 3 except *Agp-1* were heterogeneous among regions. Heterogeneity in allelic frequencies was significantly greater among than within regions ($F = 3.26$; df = 30,278; $P < 0.01$), indicating the potential of using allelic frequencies to estimate stock compositions of chum salmon in mixed stock fisheries. Heterogeneity among stocks within a region was also greater than heterogeneity between years within stocks ($F = 2.62$; df = 278, 66; $P < 0.01$).

We calculated levels of the standardized genetic variance F_{ST} (Wright 1978) among all populations for the loci at which allelic frequencies were heterogeneous. The F_{ST} values for *Idh-1*, *6-Pg*, *Me*, *Agp-2*, *Idh-3*, *Pmi*, and *Lgg* were 0.012, 0.018, 0.032, 0.033, 0.017, 0.062, and 0.094, respectively. This indicated that for these loci between 1.2 and 9.4% of the observed genetic variation was due to allelic differentiation among populations, and more than 90% of the variation was common to all populations. Levels of F_{ST} between 0.050 and 0.150 are indicative of only moderate differentiation among populations (Hartl 1980).

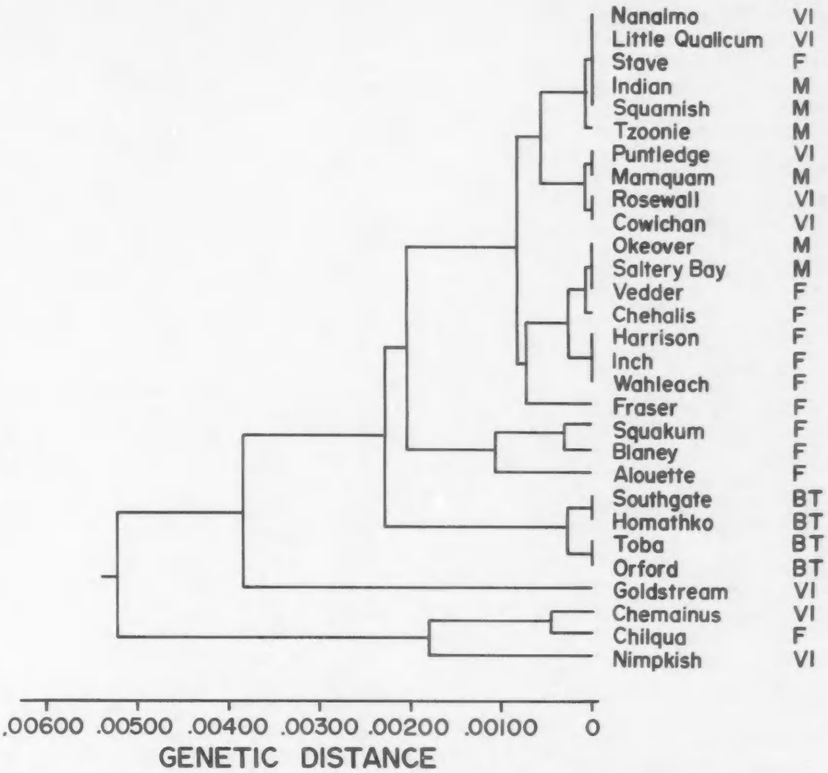

FIG. 2. Dendrogram (UPGMA, Sneath and Sokal 1973) produced using Nei's (1978) genetic distance coefficient. Codes: F = Fraser River, VI = Vancouver Island, M = Mainland, and BT = Bute and Toba inlets. Locations of stocks are indicated in Fig. 1.

Genetic distances (Nei 1978) for all pairwise combinations of the 29 stocks analyzed ranged from 0.0000 to 0.0118. Stocks from the Fraser River tended to group together, as did stocks from Bute and Toba inlets (Fig. 2). Stocks from Vancouver Island and the Mainland were interspersed in the clusters. Stocks from Nimpkish, Chemainus, and Chilqua were grouped together owing to their low frequencies of Idh-3^{100}. We also compared the mean genetic distance among chum salmon stocks within and between the four regions outlined in this study (Table 4). Chum salmon from the Fraser River were more similar genetically to those from the Mainland region than to those from Vancouver Island or Bute and Toba inlets. Chum salmon from Bute and Toba inlets were more similar to those in the Mainland region than to those in the Fraser River. Vancouver Island chum salmon were most similar to Mainland stocks, as was indicated by the cluster analysis. Stocks in the Mainland and Bute and Toba Inlet regions were more homogeneous than those in the Fraser River and Vancouver Island regions. Mean genetic distance between the stocks in the regions compared declined as the geographic distance separating the regions declined.

Heterozygosities were also compared for chum salmon stocks in the four regions. The mean heterozygosities (based upon the 10 loci in Table 1) were Fraser River (0.147, SD 0.014), Vancouver Island (0.165, SD 0.016), Mainland (0.147, SD 0.005), and Bute and Toba inlets (0.115, SD 0.006). Chum salmon from Bute and Toba inlets were less heterozygous than were stocks from the other regions.

We calculated linkage disequilibrium coefficients and tested their significance by the method of Hill (1974) for all pairwise combinations of *Idh-1*, *6-Pg*, *Me*, *Idh-3*, *Pmi*, *Lgg*, and *Agp-2* for each stock surveyed. For *Idh-3*, all alleles other than Idh-3^{100} were pooled. There were 527 separate tests conducted in the analysis, and 34 (6.5%) of these tests were significant ($\chi^2 > 3.84$, df = 1, $P < 0.05$). The method of Hill (1974) assumes that populations are in Hardy–Weinberg equilibrium, and of the 34 significant tests for linkage disequilibrium, 6 occurred when the genotypes at one locus were not in Hardy–Weinberg proportions. We conclude that there was no significant linkage disequilibrium in the chum salmon stocks surveyed.

Allelic frequencies at seven loci were found to be heterogeneous among chum salmon in the regions surveyed. The most heterogeneous grouping of stocks was the Vancouver Island region, while the least heterogeneous was the Bute and Toba Inlet region (Tables 3, 4). This may reflect the fact that Vancouver Island was the largest geographic area considered, and the Bute and Toba Inlet region was the smallest. Mean heterozygosity was also greater in Vancouver Island stocks than in stocks from Bute and Toba inlets. This may be due to zoogeographic events if the Bute and Toba Inlet stocks originated from a single founding population, whereas stocks on Vancouver Island originated from multiple founding populations. The genetic distance between the Nimpkish stock, on the north end of Vancouver Island, and the Goldstream stock, on the south end of Vancouver Island, was 0.0101, among the largest

TABLE 4. Mean genetic distance between chum salmon stocks in four regions in southern British Columbia. Number of comparisons is in the first set of parentheses and standard deviations are in the second.

Stock	Fraser River	Vancouver Island	Mainland	Bute and Toba inlets
Fraser River	0.0013(55) (0.0012)	0.0030(88) (0.0021)	0.0011(66) (0.0011)	0.0030(44) (0.0016)
Vancouver Island	—	0.0034(28) (0.0032)	0.0015(48) (0.0020)	0.0045(32) (0.0036)
Mainland	— —	— —	0.0000(15) (0.0001)	0.0022(24) (0.0010)
Bute and Toba inlets	— —	— —	— —	0.0002(6) (0.0003)

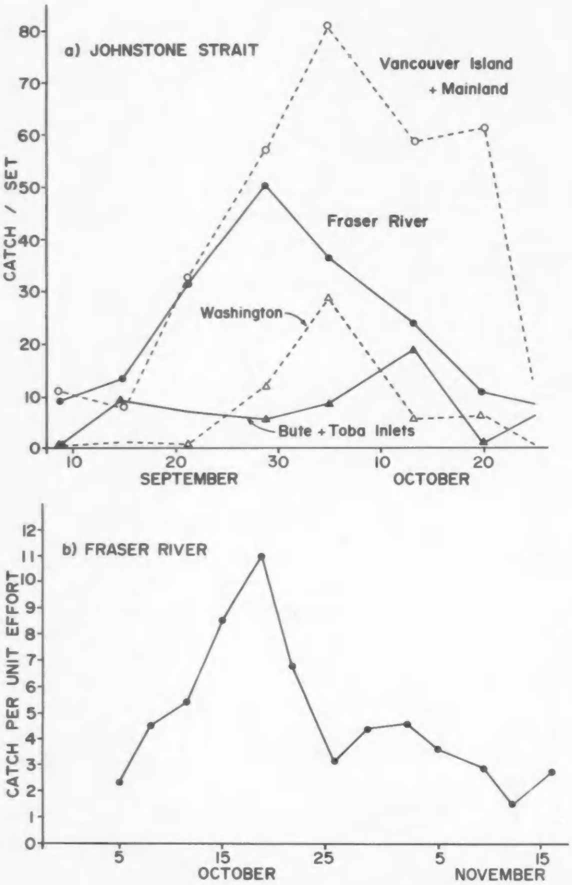

FIG. 3. (a) Mean weekly catch per set for four groups of chum salmon in the upper Johnstone Strait purse seine fishery in 1983. (b) Catch per unit effort of chum salmon in the gillnet test fishery at the mouth of the Fraser River, 1983.

for all pairwise comparisons of the stocks, and greater than would be expected on the basis of environmental differentiation. It may be that chum salmon stocks in northern and southern Vancouver Island were colonized post-glacially by genetically distinct chum salmon populations.

Heterogeneity of allelic frequencies for stocks of chum salmon in the Fraser River appear related to distance of upstream migration to the spawning grounds. Chum salmon stocks upstream from Chilqua Slough (Chehalis, Harrison, Inch, Wahleach, and mainstem Fraser) are more similar to each other than they are to downriver stocks (Squakum, Blaney, and Alouette) (Fig. 2). Upriver stocks tended to have a higher frequency of IDH-3^{100} than the downriver stocks. The similarity in allelic frequencies of the upriver stocks when compared with the downriver ones may reflect more gene flow among upstream stocks than between upstream and downstream stocks.

Levels of heterozygosity reported in our study are greater than those recorded for other chum salmon stocks (Okazaki 1982). Heterozygosity values are strongly influenced by the number of monomorphic loci included in the calculations. We did not include monomorphic loci in our calculations of heterozygosity and thus our estimates of heterozygosity will be greater than those which include monomorphic loci. Allelic frequencies of chum salmon in southern British Columbia are more similar to other North American stocks than to Asian ones for such loci as *Idh-3* and *Mdh-3,4* (Alutkhov 1981; Okazaki 1982). There are significant differences in allelic frequencies among continental populations that could be used to reliably estimate stock compositions in high seas fisheries.

Mixed Fishery Analysis

The stock identification program was initiated to estimate stock compositions of chum salmon, particularly of Fraser River origin, in fisheries in Johnstone Strait, Strait of Georgia, and the Fraser River. We sampled the upper Johnstone Strait test fishery on a weekly basis in 1983 in order to ensure that potential fisheries would not overexploit Fraser River chum salmon and to compare estimated trends in abundance of Fraser River chum salmon in Johnstone Strait with subsequent trends in abundance determined by an in-river test fishery on the Fraser River. The proportion of the sample estimated to have been derived from each region was the sum of the proportions assigned to each of the stocks within each region. The timing of the Nimpkish River stock in Johnstone Strait is much later than the other stocks surveyed (Anderson and Beacham 1983), and as it would not contribute to the weekly samples from Johnstone Strait, was excluded from the baseline samples in the stock composition analysis.

Fraser River chum salmon in Johnstone Strait reached a peak of abundance about September 28 (Fig. 3). Previous tagging analysis showed that chum salmon stocks migrating through Johnstone Strait before October 15 were recovered in the Fraser River 21 d after tagging in Johnstone Strait (Anderson and

TABLE 5. Estimated stock compositions (proportions) of chum salmon in weekly samples from a fishery in upper Johnstone Strait, September–October 1983. One hundred mixtures each containing 90% of the original sample were constructed by randomly sampling the original sample without replacement. The standard deviation of the mean proportion was derived from the 100 simulated mixtures.

Period	*N*	Fraser River	Bute and Toba inlets	Other Canadian	Washington State
Sept. 8–9	77	0.45 (0.07)	0.00 (0.00)	0.54 (0.07)	0.01 (0.01)
Sept. 14–16	101	0.42 (0.09)	0.29 (0.06)	0.25 (0.08)	0.04 (0.02)
Sept. 20–22	100	0.44 (0.08)	0.10 (0.06)	0.46 (0.07)	0.00 (0.00)
Sept. 27–30	100	0.41 (0.10)	0.04 (0.06)	0.46 (0.09)	0.10 (0.03)
Oct. 3–6	99	0.24 (0.06)	0.06 (0.06)	0.52 (0.06)	0.19 (0.03)
Oct. 10–13	100	0.23 (0.06)	0.18 (0.06)	0.55 (0.08)	0.05 (0.02)
Oct. 18–21	100	0.13 (0.05)	0.01 (0.04)	0.78 (0.06)	0.08 (0.03)
Oct. 24–26	100	0.30 (0.05)	0.23 (0.06)	0.47 (0.07)	0.00 (0.00)

Beacham 1983). The peak of chum salmon abundance in the Fraser River was about October 19 (Fig. 3), 21 d after the peak abundance of chum salmon in Johnstone Strait was estimated to have occurred. The abundance of Fraser River chum salmon migrating through Johnstone Strait increased by about a factor of five between September 8 and the peak on September 28 (Fig. 3). Chum salmon abundance in the Fraser River also increased by a factor of about five between the start of the test fishery on October 4 and the peak on October 19. The decline in abundance of chum salmon in the Fraser River after the October 19 peak was more rapid than would have been expected from the trend in abundance of Fraser River chum salmon in Johnstone Strait. The difference may be explained by two commercial fishery openings off Cape Lazo and to the southwest (Big Qualicum) on October 10–11 and October 18 in which 119 000 chum salmon were taken. A sample obtained from Cape Lazo on October 24 ($n = 100$) indicated that 36% of the chum salmon were of Fraser River origin. Chum salmon take about 14–16 d to migrate from near Cape Lazo to the Fraser River (Anderson and Beacham 1983). Chum salmon abundance in the Fraser River reached a second, smaller peak on about November 2 (Fig. 3), 2 wk after the closure of the Cape Lazo fishery, which would be coincident with the arrival of the unexploited portion of the returning Fraser River chum salmon stock. We were clearly able to determine trends in timing and abundance of Fraser River chum salmon from their entrance into Johnstone Strait through their arrival in the Fraser River.

Chum salmon from the east coast of Vancouver Island and the mainland inlets were the most abundant group of salmon in Johnstone Strait during October 1983 (Fig. 3). They comprised an estimated 78% of the salmon present during October 18–21 (Table 5). Chum salmon from Bute and Toba inlets were most abundant in Johnstone Strait during October 10–13, which suggests that the peak on the spawning grounds should be in late October or early November. The peak of abundance of Washington State chum salmon occurred during October 3–6, which suggests that they should have reached terminal fisheries in Washington in late October.

The estimates of stock compositions in the mixed fishery samples are dependent upon the accuracy of the estimates of allelic frequencies of chum salmon from the spawning grounds, the magnitude of the differences among the groups that are to be distinguished, the proportion of stocks sampled on the spawning grounds that can contribute to the mixed fishery, and the number of fish sampled in the mixtures and on the spawning grounds. In our spawning ground sampling, we examined 33 stocks, and sampled between 50 and 300 individuals from each stock. At least 100 individuals were sampled from all but two stocks. We assumed that these samples were sufficient to minimize sampling errors in our estimates of allelic frequencies. Allelic frequencies must be stable through time if the data obtained are to be used to estimate stock compositions in future mixtures. We found no significant differences in allelic frequencies between years within a stock. Allelic frequencies from other salmonids also appear to be stable (Utter et al. 1980), which indicates that it is not necessary to conduct annual surveys of spawning chum salmon stocks in order to estimate allelic frequencies.

Chum salmon stocks from the major regions surveyed in our study have significantly different allelic frequencies (Table 3), providing the potential for reliable estimation of stock compositions. The degree of reliability of our estimates may be obtained by evaluating the standard deviations of the estimates that were obtained by repeated subsampling of the original mixture (Table 5). Coefficients of variation were less for stocks comprising greater than 10% of the mixture than for those comprising less than 10%. We are clearly able to provide more reliable estimates of stock proportions for the more abundant stocks than the less abundant ones. Larger mixed fishery samples would be necessary if reliable estimates of the proportions of rare stocks are desired.

A potential problem in estimating stock compositions in a mixed fishery sample is that stocks not sampled on the spawning grounds may contribute to the mixed fishery sample. The 12 stocks that we sampled from the Fraser River comprised 91% of the 1983 chum salmon escapement to the Fraser River and its tributaries. The stocks we sampled from Vancouver Island and the Mainland inlets comprised 81% of recorded 1983 escapement in the area. We assume that the unsampled stocks have allelic frequencies similar to the stocks we sampled within the same region.

The estimated stock compositions of the weekly samples from Johnstone Strait can be evaluated in several ways. The Fraser River gillnet test fishery provides the best evidence to indicate that our weekly estimates of stock compositions in Johnstone Strait were reliable estimates of timing and abundance of Fraser River chum salmon. Our estimated early October peak in Johnstone Strait of Washington State chum salmon should have arrived in Puget Sound by mid- to late October. Catch statistics suggest that this occurred (J. Ames, Wash. Dep. Fish., Olympia, WA, pers. comm.). The 1983 peak

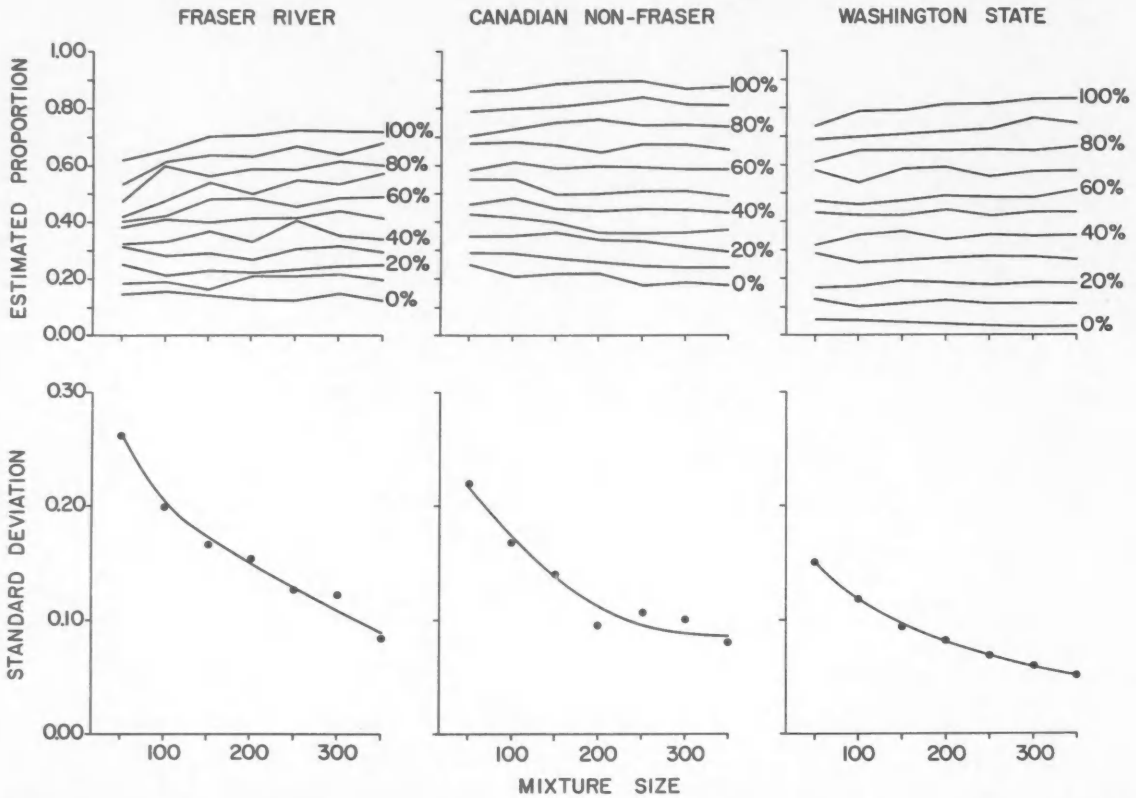

FIG. 4. Relationship between estimated stock composition, true stock composition, and mixture size for three groups of chum salmon. Fifty mixtures were constructed for each combination (77 per group) of mixture size and true proportion for each group of salmon. Estimates of standard deviation versus mixture size were obtained by determining the mean standard deviation at each mixture size for the 11 percentages investigated.

of Washington State chum salmon in Johnstone Strait occurred about 2 wk later than in 1982 (T. D. Beacham, unpubl. data), and in 1983 chum salmon in Washington arrived on the spawning grounds later than in 1982 (J. Ames, pers. comm.).

We have used genetic variation among chum salmon stocks in southern British Columbia and Washington State to provide estimates of stock compositions in fisheries in southern British Columbia. The genetic differences among stocks appear stable over time and are not subject to environmental influence, as are some morphological characters in the stocks surveyed (Beacham 1984b). When most of the stocks that contribute to a fishery have been surveyed electrophoretically, annual sampling on the spawning grounds need not be conducted. We have used electrophoresis to provide weekly estimates of stock compositions of chum salmon for use during in-season fisheries management in southern British Columbia. If sufficient genetic differences exist among stocks that are to be discriminated, electrophoretic analysis provides a valuable tool for fishery managers.

Further Applications

We examined the accuracy and precision of our estimated stock compositions by simulations for three groups of chum salmon (Fraser River, Canadian non-Fraser, and Washington State), as these are the major groups to be distinguished for fisheries management in southern British Columbia. Accuracy of the estimated proportions did not change substantially with respect to mixture size for mixture sizes in excess of 100 fish (Fig. 4). Standard deviations of the estimates declined as mixture size increased. At the same mixture size, standard deviations were largest for the Fraser River proportions and smallest for the Washington State proportions. We can estimate more precisely the proportions of Washington State and British Columbia chum salmon stocks than we can the proportions of British Columbia stocks by region.

The bias of the estimated stock compositions is greatest when stocks comprise very low or high proportions of the mixture (Fig. 5). The estimated weekly Canadian non-Fraser proportions in the 1983 Johnstone Strait fishery were generally between 55 and 75% (Table 5), a level at which reasonable accuracy and precision of the estimates are available. The estimated weekly Washington State component was always less than 20% in the Johnstone Strait fishery, and accurate and precise estimates of weekly abundance of those stocks were likely obtained (Fig. 5). The bias of the estimate of Fraser River proportion increases as Fraser River chum salmon comprise less than 10% or more than 50% of the sample (Fig. 5). In the simulations, Fraser River chum salmon in the mixtures could have been derived from 11 stocks (Weaver Creek deleted), and the bias in the estimates of the Fraser River proportion may be greater than actually observed in mixed fishery samples from

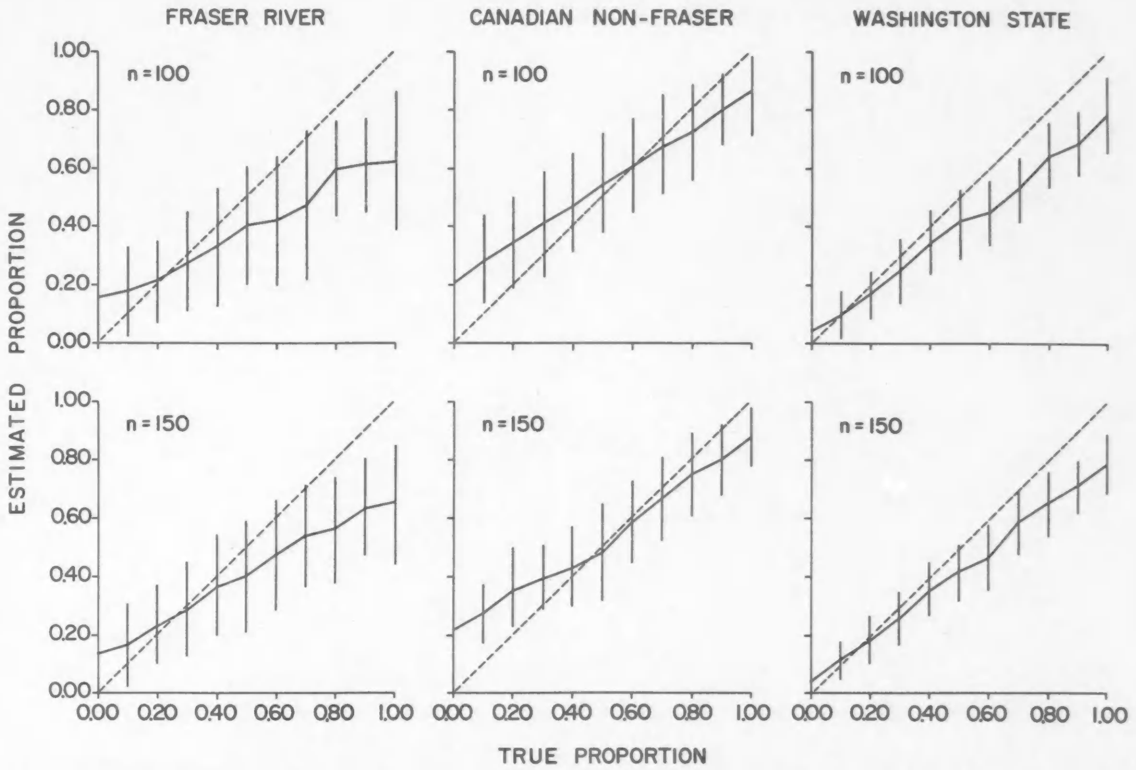

FIG. 5. Estimated versus true proportions of Fraser River, Canadian non-Fraser, and Washington State chum salmon for mixture sizes of 100 and 150 fish. The estimated proportion is the mean derived from 50 mixtures constructed at each of 11 known proportions. Vertical bars indicate 1 standard deviation.

Johnstone Strait where a restricted number of stocks was likely present at any one time. We estimated stock compositions in fisheries off the mouth of the Big Qualicum River during 1981–84. Fraser River chum salmon were not expected in this area (Anderson and Beacham 1983), and the estimated proportion of Fraser River chum salmon in these fisheries ranged from 1 to 8% (T. D. Beacham, unpubl. data). In this fishery also, we are likely able to provide more accurate estimates of Fraser River chum salmon proportions than our simulations would suggest. The agreement between the estimated Fraser River chum salmon abundance in Johnstone Strait and subsequent abundance in the Fraser River suggests that errors in our estimated proportions of Fraser River chum salmon were not large enough to obscure trends in abundance.

The accuracy and precision of the estimated stock compositions are dependent upon mixture sample size and the magnitude of the differences in the allelic frequencies of the loci used in stock discrimination. The discovery of additional loci that differ significantly in allelic frequencies between the Fraser River and Canadian non-Fraser stocks would increase the accuracy and precision of the estimated stock compositions.

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Lake Michigan's Capacity to Support Lake Trout (*Salvelinus namaycush*) and Other Salmonines: An Estimate Based on the Status of Prey Populations in the 1970s[1]

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Eck, G. W., and E. H. Brown, Jr. 1985. Lake Michigan's capacity to support lake trout (*Salvelinus namaycush*) and other salmonines: an estimate based on the status of prey populations in the 1970s. Can. J. Fish. Aquat. Sci. 42: 449–454.

We used a mass balance equation relating total mortality of age II and older alewives (*Alosa pseudoharengus*) to their removals by predatory fish and other sources of mortality as the basis for estimating that the forage base in Lake Michigan could support an additional 13 000 to 21 000 *t* of lake trout (*Salvelinus namaycush*) or a total lake trout biomass between 15 000 and 23 000 *t*. This biomass estimate is projected with biomasses of other trout and salmon held at 1979 levels. Major premises of this approach are that (1) the sustained availability of age II and older alewives to salmonines will ultimately limit the expansion of salmonine stocks, (2) the alewife population was oscillating without trend during 1973–80, and (3) additional limited predation on alewives would be compensated by a reduction in natural mortality caused by physiological stress and disease.

Une équation de l'équilibre des masses liant la mortalité totale de gaspareaux (*Alosa pseudoharengus*) âgés de deux ans ou plus à leur prélèvement par des poissons prédateurs ou d'autres facteurs de mortalité a été utilisée comme base dans l'estimation suivante : le stock en poissons fourrages présents dans le lac Michigan pourrait soutenir de 13 000 à 21 000 t supplémentaires de touladi (*Salvelinus namaycush*) ou une biomasse totale de 15 000 à 23 000 t. Cette estimation a été déterminée à partir des biomasses d'autres espèces de truites et de saumons maintenues aux niveaux de 1979. Cette approche repose sur les principes suivants : (1) la disponibilité soutenue de gaspareaux âgés de deux ans ou plus comme proies pour les salmonidés limitera en fin de compte l'expansion des stocks de salmonidés, (2) la population de gaspareaux a oscillé sans tendance de 1973 à 1980 et (3) une prédation limitée accrue du gaspareau serait compensée par une baisse de la mortalité naturelle due au stress physiologique et aux maladies.

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In Lake Michigan's greatly altered predator–prey system, large stocks of coho salmon (*Oncorhynchus kisutch*), chinook salmon (*O. tshawytscha*), steelhead trout (*Salmo gairdneri*), brown trout (*S. trutta*), and lake trout (*Salvelinus namaycush*) rely heavily on alewives (*Alosa pseudoharengus*) and to a lesser extent on rainbow smelt (*Osmerus mordax*) and slimy sculpins (*Cottus cognatus*) for food. Of these species, only the lake trout and slimy sculpin are native. This system is potentially unstable because, although some of the trout and salmon reproduce naturally, recruitment to their populations is currently maintained primarily by annual plantings of hatchery-reared young, and is largely independent of their food supply (Eck and Wells 1983). The possibility that predation may severely depress prey fish stocks in Lake Michigan cannot be overlooked if salmonine plants are further augmented by larger numbers of natural recruits or are continually increased in size (Stewart et al. 1981). Estimates of the capacity of Lake Michigan to sustain additional numbers of predators are therefore needed so that fishery managers can adjust predator stocking rates to use fully but not endanger the forage base.

Our purpose was to develop a model for estimating the maximum lake trout biomass that Lake Michigan can support at prey population levels of the 1970s, provided also that other salmonine populations were not increased in size beyond those of 1979. We emphasized lake trout because, as the only native climax predators in the present assemblage of salmonines, they have the potential for becoming self-sustaining on a large scale.

Before their extinction by sea lampreys (*Petromyzon marinus*) during the 1950s, the native stocks of lake trout in Lake Michigan supported the world's largest fishery for the species (Brown et al. 1981). Recovery of this lost lake trout resource by reestablishing self-sustaining populations is the goal of a continuing state and federal program that began in Lake Michigan during the 1960s (Smith 1968). In this program, sea lamprey control and plantings of young lake trout (mostly yearlings) are used as the principal means of rebuilding spawning stocks. Although evidence of successful natural reproduction has been meager thus far (Brown et al. 1981), the cooperating agencies plan to pursue the goal of a rehabilitated lake trout resource more intensively in the future (U.S. Fish and Wildlife Service, unpubl. information) by imposing greater restrictions on the catch of lake trout in sport and commercial fisheries and by increasing stocking rates.

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Modeling Rationale and Methods

Our modeling approach assumed that lower trophic-level dynamics are integrated by the vertebrate forage base, which we used as a more direct indicator of the lake's capacity to support salmonines. In this approach, total annual mortality of a theoretical prey fish species was equated in a mass balance equation to the sum of individual biomasses of the prey consumed by predators and extracted by other processes. The instantaneous total mortality rate (Z) of the prey population was first set equal to the sum of the component mortality rates into which it can be partitioned:

$$(1)\quad Z = M_1 + M_2 + \ldots + M_n + F + A + \theta$$

where M_i = prey mortality rate induced by the ith predator for $i = 1, 2, \ldots, n$, F = rate of fishing mortality on the prey, A = prey mortality rate resulting from water withdrawal for power generation and other uses, and θ = prey mortality rate from other causes such as physiological stress and disease. Each component mortality rate in equation (1) was then equated to the biomass of the prey species consumed or otherwise extracted annually from the population by that specific cause, divided by the mean annual biomass ($\bar{B}$) of the prey, and by substitution:

$$(2)\quad Z = \frac{1}{\bar{B}}(C_1 + C_2 + \ldots + C_n + Y + L + U)$$

where C_i = annual biomass of prey consumed by the ith predator, Y = annual yield to the fishery, L = annual biomass lost to entrainment and impingement at water intakes, and U = annual biomass lost to "other" forms of natural mortality.

In this generalized form, however, equation (2) has no special predictive qualities, and its terms are extremely difficult to interpret at the species population level. Mortality schedules of various life stages that compose the total population are either independent or interrelated in complex ways difficult to evaluate. They are also difficult or, for early life stages of alewives or smelt, impossible to measure accurately with current state-of-the-art sampling methodologies (Brandt et al. 1980; Hatch et al. 1981). We therefore modified and rearranged terms in equation (2) so that it could function for a given life stage or combination of age groups of a given species:

$$(3)\quad \bar{Z}\bar{B} = C_1 + C_2 + \ldots + C_n + \bar{Y} + \bar{L} + \bar{U}$$

where $\bar{Z}$ = average mortality rate of the designated portion of the prey population, weighted by each age group's relative numerical contribution to that portion of the population, and other parameters are as previously defined except that they now pertain only to the designated portion of the stock.

This equation's utility with respect to modeling the predator–prey system in Lake Michigan during the 1970s was based on two major premises: first, that the availability of age II and older alewives largely dictated the lake's carrying capacity for salmonines, and second, that alewives in Lake Michigan were in a long-term state of equilibrium in the sense that the population was oscillating about a mean level without trend. Fish ≥ age II include the adult part of the alewife population and large numbers of pre-adults in age groups II and III, most of which are pelagic (Fig. 1). Because some components of alewife mortality in Lake Michigan are probably compensatory, we hypothesize that alewife population size, as measured by its 1973–80 mean, would not be disrupted if limited numbers of salmonines were added to the predator population.

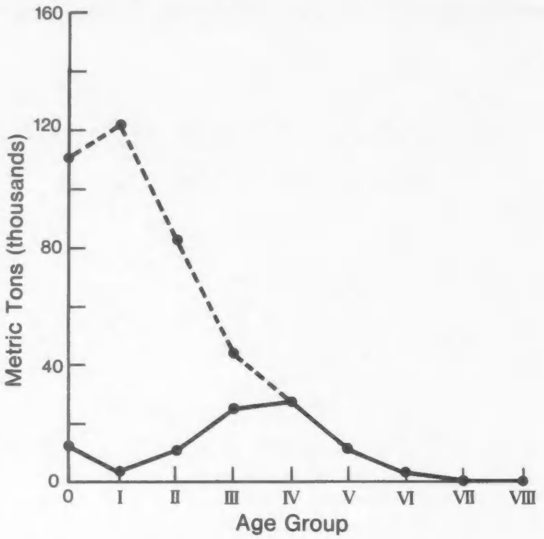

FIG. 1. Average annual biomass by age groups for Lake Michigan alewives during fall 1973–80; the biomass of fish available to trawls (solid line) is further expanded to adjust for lower vulnerability to the gear in age groups 0–III (broken line). Data from Brown (unpubl. data).

Availability of Age II and Older Alewives — A Limiting Factor

Alewives in general, and those age II and older in particular, were by far the most important part of the forage base for salmonines in Lake Michigan during the 1970s. Eck and Wells (1983) estimated that about 51% by weight of fish eaten by the Lake Michigan lake trout population during the 1979 growing season were alewives age II and older (71% were alewives of all ages). Moreover, Stewart et al. (1981) estimated that coho and chinook salmon were even more dependent than lake trout on "adult" alewives, which constituted about 55–80% by weight of the total food consumed annually by those respective salmonines. Note that Stewart et al. (1981) classified all alewives of age I and older as adults, whether or not they were sexually mature. Although data are not available on food of steelhead and brown trout, it is almost certain that these species also feed heavily on alewives age II and older. In retrospect, then, no other extant prey species or combination of species appeared capable of matching these older alewives as forage for lake trout and salmon in Lake Michigan; this situation led to our premise that the older alewives were, and would probably continue to be, the main determinant of the lake's carrying capacity for those predators.

Alewives and other clupeoids are noted, however, for abrupt changes in population size (Brown 1968, 1972; Adams et al. 1982). The biomass of alewives available to bottom trawls in Lake Michigan has varied since 1967, for example, by a factor of 2 from one fall sampling period to the next (Hatch et al.

1981), and year-class strength has varied by a factor of 2.9 (E. H. Brown, Jr., unpubl. data).

Brown (unpubl. data) considers that alewife stock size is determined by a combination of density-dependent and density-independent conditions, but did not attempt to quantify the importance of one relative to the other. He suggested, however, that temperature stress on alewives in Lake Michigan is intensified at high population density because of lower mean body weight at length (i.e. an indication of lower energy reserves). MacCall (1980), on the other hand, suggested that density-independent influences are theoretically 10 times more important than density-dependent factors in determining stock size for clupeoids of the genus *Engraulis*. Because of this preponderance of density-independent effects, MacCall suggested that an engraulid stock does not reach a narrowly bounded equilibrium. Instead, population abundance fluctuates considerably over the years, forming a probability distribution about its mean.

During the decade of the 1970s and earlier, the change in abundance of the alewife in Lake Michigan closely followed the description by MacCall (1980) of the behavior of engraulid populations. Alewives invaded Lake Michigan in the late 1940s and underwent a population explosion in the early 1960s that culminated in a mass lakewide die-off in 1967 (Brown 1972). The stock gradually regained some of its former size in the late 1960s and early 1970s but peaked at a reduced level in the 1970s. From 1973, when lakewide sampling began, through 1980, the size of the population oscillated between that of 1967 and a secondary peak in 1975, showing no evidence of a sustained increase or decrease (Fig. 2). For modeling purposes, we thus assumed that mean population size in 1973–80 represented an average equilibrium level of abundance for alewives because their performance in Lake Michigan strongly suggested that that value was the best indicator of future population size. The assumption of an average equilibrium level of abundance was further supported because annual losses in biomass of age II and older alewives during 1973–80 appeared to have been replaced on the average by recruitment plus production by those age groups (Table 1). During this period, average annual biomass of age II and older alewives lost to deaths (i.e. $\bar{Z}\bar{B}$ in equation (3)) was 137 000 t, compared with a combined mean annual recruitment and production of about 129 000 t.

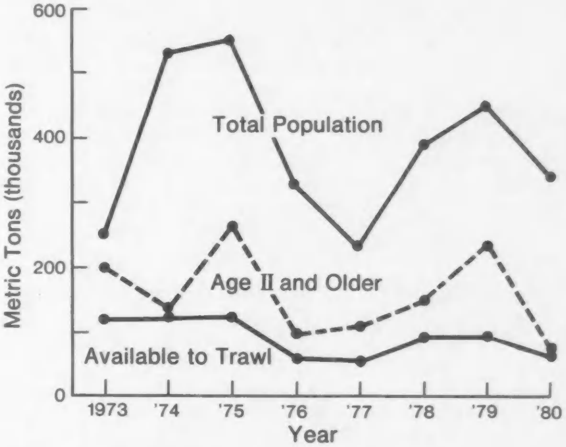

FIG. 2. Annual biomass of Lake Michigan alewives during fall 1973–80, estimated as the product of catch per unit area in bottom trawls and total area, expanded further to adjust for lower vulnerability to the gear of age groups 0–III. Data from Brown (unpubl. data).

TABLE 1. Mean annual production of age II and older alewives in Lake Michigan and mean recruitment to the population at age II, 1973–80[a].

Age	Metric tons (thousands)		
	Production	Recruits	Combined
II	33.7	81.4[b]	115.1
III	8.0	—	8.0
IV	4.1	—	4.1
V	1.6	—	1.6
VI	0.4	—	0.4
VII	0.1	—	0.1
Total	47.9	81.4	129.3[c]

[a] Adapted from Brown (unpubl. data).

[b] As of May 1.

[c] Note that $\bar{Z}\bar{B} = 0.867 \times 158.0\,\mathrm{t} = 137.0\,\mathrm{t} \simeq 129.3\,\mathrm{t}$.

The Model — Compensation Among Mortality Components

In theory, the component rates of mortality had to remain relatively constant to maintain the rough equilibrium of age II and older alewives in the 1970s, assuming of course that the rates are independent and additive as viewed in conventional fishery models. If, for example, the combined rate at which salmonines eat the older alewives changes, $\bar{Z}$ also changes and the alewife population will move to a different biomass level and possibly a new equilibrium. We doubted, however, that the assumption of independence among component mortality rates applies to the alewife in Lake Michigan, and considered instead that a limited increased rate of predation would not necessarily result in a disruption of the alewife population's equilibrium.

In a schooling species like the alewife, individuals that exhibit aberrant behavior stand a greater risk of being eaten by a predator than do those that behave normally (Radovich 1979; Hobson 1968). Also, because most kinds of physiological dysfunction (e.g. disease) are usually manifested by behavioral changes, it follows that unhealthy individuals are preferentially selected as prey. The rate of this "culling" process should accelerate as predator density increases relative to that of the prey because of corresponding increases in the chance of an aberrant individual being encountered and eaten. Therefore, the quantity U, representing all other causes of mortality in equations (2) and (3), is not necessarily an independent mortality component, but more likely bears an inverse or compensatory relation to the rate of predation. Theoretically, predation is thus a substitute form of mortality, and consumption of prey by predators

$$\left(\text{i.e. } \sum_{i=1}^{n} C_i\right)$$

could be increased at the expense of U without disrupting the population equilibrium.

Stated another way, θ in equation (1) should perhaps be redefined as the rate at which age II and older alewives develop or acquire physiological dysfunctions. This rate may indeed be independent of component mortality rates, but the chances of a fish dying and being lost to the next highest trophic level after contracting a disease depends on whether it is eaten before death or scavenged after death. Granted, some of these fish may be lost and contribute to U regardless of predator density and the degree to which they are preferentially selected as prey. For example, death may occur outside the predator's depth range, or predators may become satiated if deaths due to θ are seasonally pulsed. Thus, predation would probably never completely replace U as a mortality component.

Alewife Biomass and Production

Data on alewife biomass and production, together with vital statistics, were obtained for this study from a concurrent population study on the alewife, in which Brown (unpubl. data) estimated age-specific production as the product of instantaneous growth (G) and mean biomass ($\bar{B}$), using vital statistics from lakewide surveys of the forage base with a 12-m bottom trawl in October and November 1973–80. He estimated seasonal biomasses and production directly for the fully available (on a relative basis) part of the fishable stock ($\geqslant$age IV) and theoretically for the younger, partly available ages, using indirect methods.

Forage Fish Consumption by Salmonines

We obtained estimates of the biomasses of prey consumed by each year class of lake trout in Lake Michigan in 1979 from a related study by Eck and Wells (1983), who estimated consumption by dividing each cohort's production ($\bar{G}\bar{B}$) by the corresponding age-specific food conversion efficiency determined in the laboratory. They estimated biomasses of trout with which to compute production by predicting the number of survivors remaining from each year-class planted from 1966 through 1978, using an instantaneous total mortality rate (Z) of 0.65 equivalent to an average annual rate of 0.48 for all ages of lake trout. The numbers of survivors at each age were then multiplied by their predicted mean weights to estimate biomass. Species composition of the total biomass consumed by the lake trout was estimated from mean percentages of the three prey species, alewives, rainbow smelt, and slimy sculpins, in the diet of lake trout sampled in southern Lake Michigan in 1976–77. The complete series of calculations for any given life stage (age) of lake trout is summarized by the equation $C = (G\bar{B}/E) \times D$, where C = metric tons of a given prey consumed, E = food conversion efficiency of given life stage of predator eating prey, and D = fraction of the prey species in natural diet of the predator.

The estimated biomasses of prey consumed by salmon and steelhead and brown trout were obtained from Stewart et al. (1981, 1983), who used an energetics model based on experimental data supplemented by theoretical assumptions to bridge various information gaps. We estimated the corresponding biomasses of these salmonids, like those of lake trout, from the numbers of survivors at each age from the various plants (Great Lakes Fishery Commission 1980, 1982a, 1982b) as determined from estimated or theoretical survival rates.

Projected Capacity of Lake Michigan to Support Lake Trout and Other Salmonines

We used equation (3) as the basis for predicting the maximum biomass of salmonines that a forage base comparable with that extant in Lake Michigan in the 1970s can support. Estimates of $\bar{Z}$, $\bar{B}$, $\bar{Y}$, and $\bar{L}$ were computed as mean values for 1973–80 data, in accordance with the earlier conclusion that average population characteristics of alewives in this period of comparative stability are the best indicators of these values in the near future. Annual population statistics derived by Brown (unpubl. data) were used to estimate $\bar{Z}$ (0.867) and $\bar{B}$ (158 000 t); catch statistics of the commercial fishery for alewives (Great Lakes Fishery Laboratory (GLFL), unpubl. data) during 1973–79 (the 1980 catch was excluded because of an atypical reduction in fishing effort due to depressed markets and chemical contamination of alewives) were used to estimate $\bar{Y}$ (18 000 t); and a relation developed by Jensen et al. (1982) was modified to reflect Brown's higher estimate of adult alewife biomass in the Lake, and used to estimate $\bar{L}$ (1300 t).

We used the estimated biomasses of age II and older alewives that were consumed (C_i) in 1979 and of the lake trout population extant in Lake Michigan during that year to project the additional lake trout biomass that could be supported. Eck and Wells (1983) estimated that lake trout, having a biomass of 1600 t at the start of the year, ate about 1500 t of the older alewives during the 1979 growing season for lake trout in Lake Michigan (i.e. May 15 to December 1). We expanded this estimate by 33% (2000 t) to include an estimate of consumption during winter and early spring when lake trout feed at a reduced rate (Stewart et al. 1983; GLFL, unpubl. data). An estimate of the total biomass of alewives eaten by all other salmonines combined in Lake Michigan during 1979 was obtained from Stewart et al. (1981, 1983) by subtracting their estimate for lake trout from the total given for all the salmonines (Stewart et al. (1981) did not indicate the quantities of alewives consumed by the other predator species individually). Although the resulting value (40 000 t) was used in our calculations, it somewhat overestimates the annual consumption of older alewives by other salmonines, because it includes alewives younger than age II that were also eaten by those predators.

Using the foregoing parameter estimates for the older alewives and their predators as input, we estimated the maximum additional lake trout biomass that Lake Michigan could theoretically support from the following relation: $\Delta B_1 = U/C_1 \times B_1$; where $U = \bar{Z}\bar{B} - (C_1 + C_2 + \bar{Y} + \bar{L})$, a shortened transposition of equation (3); B_1 = estimated biomass of lake trout at beginning of 1979; C_1 = estimated biomass of alewives $\geqslant$ age II eaten by lake trout in 1979; and C_2 = estimated biomass of alewives $\geqslant$ age II eaten by other salmonines in 1979. Actually, however, we expected that recruitment to the alewife stock would undoubtedly continue its characteristic annual fluctuations, and U would probably never be totally replaced by predation as implied by the above equation. We therefore used the lower 95% confidence limit of the mean biomass of age II and older alewives in 1973–80 as a more conservative and prudent estimate of the available biomass than the mean ($\bar{B}$) itself. This safeguard reduced the estimated mean annual biomass of alewives $\geqslant$ age II from 158 000 to 101 000 t and led to the final estimate of U and thence ΔB_1. Therefore, if C_1, $\bar{Y}$, and $\bar{L}$ remained the same as in recent years, U = 87 600 t − 61 300 t and ΔB_1 = 13 × 1600 t or 21 000 t (rounded to nearest thousand metric tons). The maximum lake trout biomass that Lake Michigan could have hypothetically supported is therefore equal to $B_1 + \Delta B_1$, or about 23 000 t.

Because the value of ΔB_1 is extremely sensitive to estimates of the amount of older alewives consumed, we recalculated consumption using estimates of lake trout production by cohort from Eck and Wells (1983) and age-specific lake trout food conversion efficiencies from Stewart et al. (1983). Eck and Wells based their consumption estimates on food conversion efficiencies derived for lake trout on ad libitum rations in the laboratory. Rations and conversion efficiencies are probably lower in the wild, suggesting that the consumption estimates of Eck and Wells (1983) are possibly minimum values. The much lower conversion efficiencies that Stewart et al. (1983) estimated indirectly for Lake Michigan lake trout using an energetics model result in an estimate of about 3000 t of older alewives consumed, an increase of 50%. Substitution of this value in our previous calculations lowered our estimate of maximum sustainable lake trout biomass to 15 000 t. This estimate, our original estimate, and the 12 000 t estimate for the mean annual biomass of other trout and salmon thus represent a theoretically sustainable biomass of salmonine predators ranging from 27 000 to 35 000 t.

The additional assumptions implicit in these estimates are that (1) plants of the other salmonines would be maintained at their pre-1979 rates and (2) predator growth and mortality, as well as the proportions of age II and older alewives in the diets of the various salmonine species, would remain constant as predator density was increased. Realistically, values of the parameters contained in the second assumption are likely to change with increasing predator density. The amount of change in these values at the projected maximum predator biomass might not be large, however, because of our overestimate of the amount of older alewives eaten by salmonines other than lake trout, and use of the lower 95% confidence limit of mean annual biomass of the older alewives.

Discussion

The maximum lake trout biomass of 23 000 t (3.97 kg/ha) that we projected in this study on the basis of forage levels of the 1970s is high in comparison with a conservative estimate (Brown et al. 1981) that 13 000 t (2.24 kg/ha) would have been necessary to produce the reported average annual yield to the historical fishery of 2600 t in 1927–44 (GLFL, unpubl. data). Because of decades of heavy exploitation, however, the lakewide population of native lake trout was probably substantially smaller in 1927–44 than it was before fisheries developed in the 1800s. Early reports of Milner (1874), Smith and Snell (1891), and Smith (1908) suggest that various stocks were sequentially overfished in Lake Michigan beginning in the mid-1800s. This process would have been aided by technological advances, especially in the power sources of fishing vessels.

The productivity of the recent alewife-dominated forage base, as compared with that of the endemic fish community in which ciscoes (*Coregonus* spp.) were dominant, provides another key as to whether Lake Michigan could actually have supported our projection for lake trout and other salmonines combined. Alewives, for example, have provided far greater yields to commercial fisheries than the ciscoes ever did (Baldwin et al. 1979), they produce about 8 times more eggs per gram of body weight than ciscoes (Emery and brown 1978; Hlavek and Norden 1978), and do not grow beyond sizes suitable as prey for adult trout and salmon. We believe, therefore, that the altered prey fish assemblage produced more potential forage for predators in the 1970s than did the endemic assemblage present before the sea lamprey invasion.

Despite the possibility that it was more productive, the forage base of the 1970s — the one used in this study to project maximum biomasses of lake trout and other salmonines that Lake Michigan could support — has changed substantially in the 1980s. Fall bottom trawl surveys (GLFL, unpubl. data) yielded minimum biomass estimates of 118 000, 15 000, and 9000 t, respectively, for alewives, rainbow smelt, and bloaters (*C. hoyi*) in 1973 as compared with estimates in 1983 of 30 000 t of alewives, 22 000 t of rainbow smelt, and 141 000 t of bloaters. Thus, alewife abundance has rapidly declined while that of smelt and bloaters has continued to increase, the latter quite dramatically, although significant numbers of bloaters have not yet been detected in the diet of lake trout as a result (GLFL, unpubl. data). The salmonines have undoubtedly helped to moderate alewife abundance (Stewart et al. 1981), but changes in the thermal environment since about 1976 may be exerting even stronger control in Lake Michigan and also in Lake Huron, according to long-term observations in both lakes.

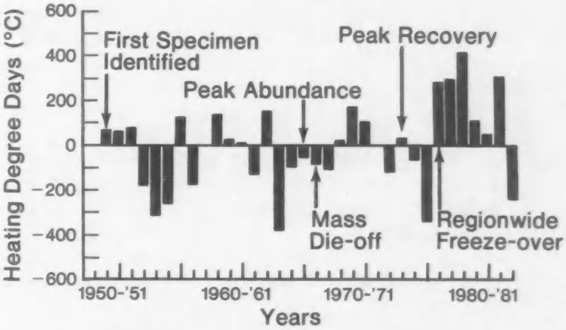

FIG. 3. Deviation from mean (1949–83) heating degree days recorded for the July 1 to July 1 heating season each year by the National Weather Service at Muskegon, Michigan (NOAA 1949–83). Note that positive deviations indicate colder than average heating seasons. Air temperature at the Muskegon Weather Station is probably mediated more by Lake Michigan than is air temperature at any other weather station in the region.

The winter of 1976–77 seemingly marked the beginning of a series of annual periods that were much colder than those previously experienced by alewives in Lake Michigan (Fig. 3). (The uncommon simultaneous occurrence of lakewide ice cover was observed on all five of the Great Lakes in February and March of 1977.) Because alewives are believed to be sensitive to cold (Colby 1973), low-temperature stress has been suspected as a contributing factor in alewife die-offs that have occurred with some regularity in Lake Michigan since the mass die-off in 1967. Colby (1973) even suggested that the more commonly observed die-offs of alewives in spring and summer are delayed responses to cold stress over winter. Colder than average annual temperature cycles in the 1970s may also have affected alewife year-class strength by shortening the growing season and hence leading to the production of smaller young-of-the-year more vulnerable to cold stress. Brown (unpubl. data) estimated that average winter mortality of young alewives was about 81% during 1973–79 and concluded that such mortality was size selective and highest among the smallest young of each year-class.

The impact that these severe winters may have had on alewives cannot be fully assessed until each year-class that experienced them becomes fully available to trawls at age IV. If this impact was as strong as preliminary information suggests, the secondary peak in our expanded alewife biomass curve is exaggerated (Fig. 2) and our estimates of maximum salmonine biomass that Lake Michigan could have supported are too high.

We suggest, however, that changes in the physical environment, and not current levels of predation, have been primarily responsible for the recent decline in size of the alewife population.

If the annual temperature regime remains cooler than average, as it did with only one exception during 1976–83 (Fig. 3), we predict that the Lake Michigan alewife population will continue to decline and perhaps eventually resemble the present Lake Superior population. Alewives have never become abundant in Lake Superior's cold environment, since invading that lake in the mid-1950s. However, the species has persisted in Lake Superior. We doubt therefore that Lake Michigan will ever become cold enough to eliminate alewives. The remnant stocks should instead undergo a resurgence in abundance in Lake Michigan if thermal conditions become as moderate as they were in the 1950s and 1960s.

Although we believe that predation did not trigger the recent downward trend in alewife abundance, predators may have speeded the decline by continuing to rely on alewives for food while abiotic factors were limiting recruitment. Based on fall trawl surveys, adult alewife biomass in Lake Michigan was reduced by a factor of 5 from 1981 to 1983. Yet, during that period, alewives composed a larger proportion of the lake trout diet than would have been expected from their proportional representation in the total of all forage fishes that were available as prey (GLFL, unpubl. data). If other salmonines behaved similarly to lake trout in Lake Michigan, antiswitching (Chesson 1978) by predators could have produced a source of depensatory mortality for adult alewives, especially when alewife abundance dipped precipitously in 1983.

Declining alewife stocks do not necessarily portend dire consequences, however, for salmonine management programs in Lake Michigan. The major implication is that the evolving forage base may not be able to sustain salmonine biomasses as large as the ones that we projected. Because the bulk of the forage base now consists of species less pelagic than alewives, lake trout, the most bottom oriented of the salmonines, should adapt to it more readily than the more pelagic chinook and coho salmon. Information on habitat partitioning among salmonines and on any habitat shifts that may be occurring in response to the changing availability of prey is needed, however, to determine the number of predators, by species, required to use the recently altered forage base efficiently.

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Discrimination d'un stock de poisson, l'anguille (*Anguilla rostrata*), basée sur la présence d'un produit chimique de synthèse, le mirex

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Le dosage du mirex dans des anguilles (*Anguilla rostrata*) en provenance de l'Est du Canada nous a permis de mesurer la contribution du stock d'anguilles du lac Ontario dans la pêche commerciale du Saint-Laurent. Toutes les anguilles échantillonnées dans le lac Ontario (50 spécimens) contenaient du mirex (0,18 ± 0,11 $\mu g \cdot g^{-1}$). Les anguilles résidentes échantillonnées dans la pêche commerciale du Saint-Laurent, de même que les anguilles migratrices ou résidentes échantillonnées dans des tributaires du Saint-Laurent et dans les Maritimes, ne contenaient généralement pas de mirex. Par contre, 74 % des anguilles en migration catadrome en contenaient (0,17 ± 0,19 $\mu g \cdot g^{-1}$). Nous pensons qu'il est possible de distinguer des stocks de poissons sur la base de la présence de pesticides ou d'autres contaminants de synthèse à distribution restreinte dans l'environnement. Puisqu'elle est basée sur un critère absolu de présence–absence dans les animaux et dans l'environnement, la nouvelle méthode présente l'avantage d'être plus précise et plus rapide que les méthodes de discrimination des stocks basées sur la présence de produits chimiques naturels.

Mirex concentrations were measured in eels (*Anguilla rostrata*) from eastern Canada to determine the contribution of Lake Ontario eels to the Saint Lawrence commercial fishery. Mirex could be detected in all eels (50 specimens) collected in Lake Ontario (0.18 ± 0.11 $\mu g \cdot g^{-1}$). Most sedentary eels collected from the Saint Lawrence commercial fishery and both the migratory and sedentary eels collected from the Saint Lawrence tributaries and the Maritimes had no mirex. Of the migrating eels collected in the Saint Lawrence 74% contained mirex (0.17 ± 0.19 $\mu g \cdot g^{-1}$). These results show that stocks can be discriminated on the basis of the presence of synthetic chemical products such as pesticides and other contaminants that are distributed heterogeneously in the environment. Based on a presence–absence criterion, this method for stock discrimination has the distinct advantage that it is more accurate and less time consuming than similar methods based on the presence of natural chemical products.

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La notion de stock et les méthodes de discrimination des stocks sont revues par MacLean et Evans (1981) et Ihssen *et al.* (1981). Ces méthodes sont basées sur l'interprétation de la variabilité de paramètres physiologiques, méristiques, biochimiques ou génétiques, ou la reconnaissance de marques, naturelles ou non, des stocks de poissons. Les marques naturelles les plus couramment mises à contribution sont les parasites (Fréchet *et al.* 1983 ; Black 1983 ; Margolis 1965) et la teneur en minéraux des écailles, tel que montré par Bagenal *et al.* (1973) chez la truite brune (*Salmo trutta*) et par Moreau et Barbeau (1979) chez le corégone (*Coregonus clupeaformis*). Récemment, Moreau et Barbeau (1982) montraient que les concentrations de métaux lourds dans la chair des poissons pouvaient servir à la discrimination des stocks, mais la distribution généralisée des métaux lourds dans les lacs et les rivières limitait l'utilisation de la méthode aux stocks provenant de bassins montrant des écarts très marqués dans les concentrations de métaux lourds.

Nous examinons ici la possibilité de discerner un stock de poissons dans une pêche commerciale sur la base de la présence ou de l'absence d'un insecticide de synthèse dont la distribution est connue mais restreinte dans l'environnement. Le terme « stock » est entendu au sens de Larkin (1972), soit une unité de production ou de gestion de la ressource, mais la méthode est aussi valable pour les stocks au sens biologique de MacLean et Evans (1981). La pêche à l'anguille (*Anguilla rostrata*) dans le Saint-Laurent exploite un mélange de stocks provenant de l'ensemble des tributaires. L'anguille est un poisson catadrome commun dans le bassin du Saint-Laurent. Lorsqu'elle laisse les lacs et les rivières pour sa migration annuelle vers la mer des Sargasses, l'anguille en voie de maturation sexuelle donne lieu à une pêche commerciale, particulièrement dans le Richelieu et dans le fleuve Saint-Laurent entre le lac Saint-Pierre et Rimouski (fig. 1). La pêche commence au printemps dans le Richelieu et dans le lac Saint-Pierre et se déplace vers l'estuaire à mesure que l'anguille dévale vers la mer, pour se terminer à l'automne à Rimouski. La pêche est menacée par la contamination de certains stocks par le mirex. Le mirex (Windholz 1976)

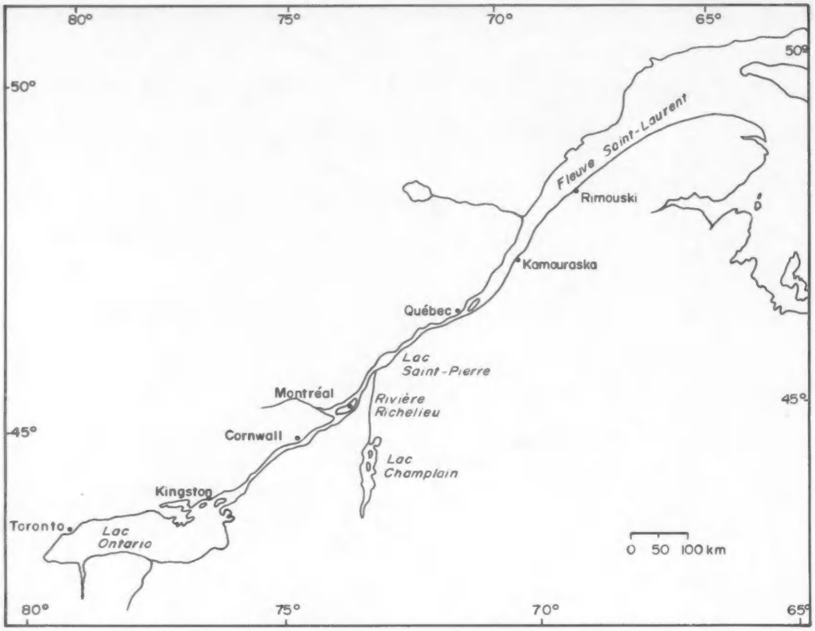

FIG. 1. Localisation des sites d'échantillonnage.

est un produit chimique très stable et insoluble dans l'eau. Il entre dans la fabrication d'insecticides pour le contrôle de la fourmi rouge (Kaiser 1978). Nous désirons démontrer dans ce travail que le mirex, comme plusieurs produits chimiques de synthèse qui contaminent l'environnement (Gilbertson 1977 ; Zitko 1980), constitue un très bon marqueur chimique des stocks de poissons.

Méthodes et matériel

Sur la base de nos connaissances de la distribution du mirex dans le bassin du Saint-Laurent (Kaiser 1978 ; Gilbertson 1977 ; Holdrinet *et al.* 1978), le territoire a été divisé en trois secteurs : A— lac Ontario et tronçon Kingston–Cornwall ; B— lac Champlain et rivière Richelieu ; C— fleuve Saint-Laurent (lac Saint-Pierre, Québec et Kamouraska). Des échantillons ont aussi été récoltés sur la Côte-Nord du Saint-Laurent (Grande rivière de la Trinité) et dans les Maritimes (Desjardins *et al.* 1983). Tous les échantillons, excluant ceux de la Côte-Nord proviennent de la pêche commerciale. L'échantillonnage des anguilles a été réalisé au hasard à même les prises de pêcheurs commerciaux localisés dans chacun des secteurs, aux dates présentées par Desjardins *et al.* (1983). Les échantillons étaient expédiés dans la glace au laboratoire, où les anguilles étaient mesurées (±1 mm) et pesées (±10 g, mais ±28 g dans le cas des spécimens de Kamouraska).

La maturité sexuelle est le critère de distinction entre les anguilles en migration catadrome et les anguilles résidentes (sédentaires). Le jugement est fondé sur le diamètre des oocytes (diamètre maximum moyen de 10 cellules dont le noyau est visible) et sur la présence ou l'absence de gouttelettes lipidiques dans le cytoplasme de ces cellules. Le poids des gonades était déterminé puis une partie de celles-ci était fixée dans la solution de Bouin, déshydratée dans le méthanol, enrobée dans la paraffine et tranchée à 8 μm. Fixées sur lames, les coupes étaient colorées à l'hématoxyline–phloxine et recouvertes d'une lamelle pour la détermination du sexe et de la maturité sexuelle (Sinha et Jones 1975 ; Tesch 1977).

Pour les analyses chimiques, les spécimens étaient éviscérés, la tête et l'extrémité caudale enlevées, puis le reste du poisson était homogénéisé à trois reprises dans un broyeur doté d'une grille dont les orifices mesuraient 3 mm de diamètre. Les homogénats ainsi obtenus étaient entreposés à −4°C dans des bocaux en verre munis de couvercles en aluminium, jusqu'à l'analyse de leur teneur en mirex (seuil de détection : $0{,}001\ \mu g \cdot g^{-1}$) selon la méthode décrite par Desjardins *et al.* (1983). Les données ont été testée par les méthodes de Mann–Whitney et Kruskal–Wallis.

Résultats et discussion

Les anguilles récoltées ont été classées anguilles migratrices ou anguilles résidentes selon le critère suivant : celles dont le diamètre moyen des oocytes était plus grand ou égal à 85,0 μm étaient considérées être en voie de maturation sexuelle et donc en migration vers la mer des Sargasses. Les autres étaient classées résidentes. Le seuil de 85,0 μm nous a semblé réaliste puisque dès le printemps (fig. 2, secteur C— lac Saint-Pierre), la distribution des fréquences du diamètre des oocytes est bimodale avec un creux se situant à 85,0 μm. Par la suite (fig. 2, secteur C— Kamouraska), le diamètre moyen des oocytes des anguilles migratrices progresse jusqu'à 210 μm en automne. Dans le secteur A, l'histogramme est aussi bimodal avec un creux à 85,0 μm, mais la distinction n'est pas très marquée si l'on considère la distribution des fréquences du diamètre pour les échantillons prélevés dans le secteur B à la même période (fig. 2). Toutes les anguilles récoltées étaient des femelles (les mâles sont très rares parmi les anguilles du bassin du Saint-Laurent). Les anguilles migratrices des secteurs A, B et C ont des longueurs et des poids homogènes ($\alpha = 0{,}05$) (tableau 1).

TABLEAU 1. Statistiques biométriques des anguilles échantillonnées, par secteur : A— lac Ontario et tronçon Kingston–Cornwall ; B— lac Champlain et rivière Richelieu ; C— lac Saint-Pierre, Québec et Kamouraska. ($\bar{L}$ = longueur moyenne, $\bar{P}$ = poids moyen, $\overline{\text{D.O.}}$ = diamètre moyen des oocytes, s = écart-type, taille de l'échantillon entre parenthèses.)

Secteur	Statut	$\bar{L} \pm s$ (mm)	$\bar{P} \pm s$ (g)	$\overline{\text{D.O.}} \pm s$ (μm)
A	Migratrices	836±62 (10)	1505±404 (10)	99,6±12,9 (10)
	Résidentes	749±83 (40)	939±318 (40)	68,6±8,6 (40)
B	Migratrices	847±77 (39)	1315±412 (39)	129,2±12,2 (39)
	Résidentes	744 (1)	701 (1)	49,2 (1)
C	Migratrices	843±103 (339)	1357±533 (338)	171,1±42,8 (342)
	Résidentes	648±61 (20)	446±115 (20)	65,4±8.5 (20)

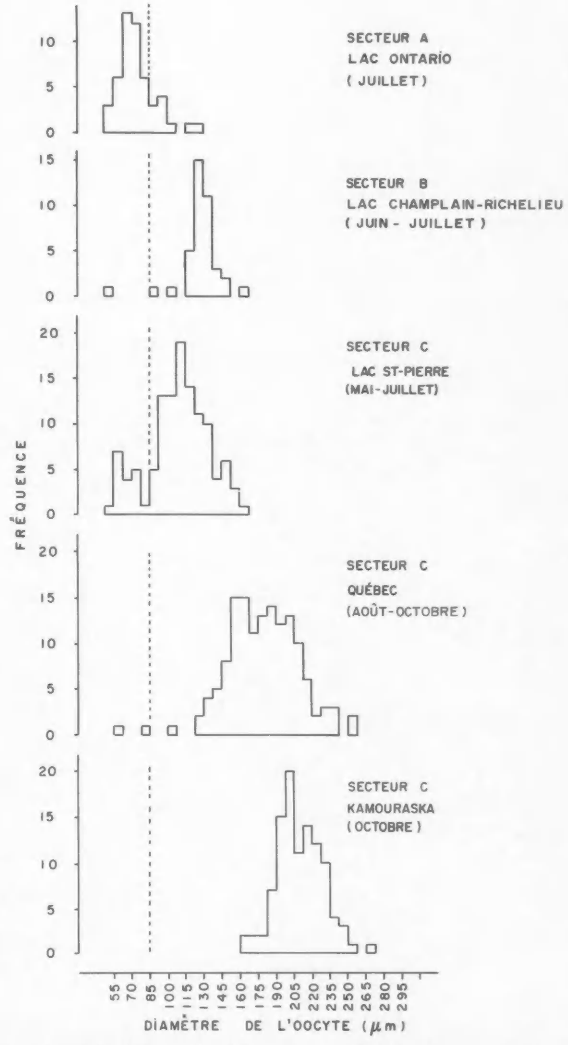

FIG. 2. Distribution des fréquences du diamètre des oocytes par secteur. La ligne en traits représente la limite séparant les anguilles résidentes et les anguilles migratrices.

Les anguilles recueillies dans le secteur A contenaient toutes du mirex (tableau 2), mais à des concentrations très variables puisque le nombre d'années passées par les anguilles au contact de sédiments contaminés et les taux de contamination des sédiments sont très variables. La concentration de mirex dans les anguilles est très élevée : 0,18 ± 0,11 $\mu g \cdot g^{-1}$ (migratrices et résidentes). La présence de mirex dans toutes les anguilles, particulièrement les 40 anguilles résidentes, reflète la présence de ce produit chimique dans le secteur A. Le lac Ontario est le seul parmi les Grands Lacs à être contaminé par le mirex (Kaiser 1978). Déjà en 1968, les sédiments de la moitié sud du lac étaient contaminés. Les déversements ont eu lieu jusqu'en 1972 dans les tributaires Niagara et Oswego (Gilbertson 1977 ; Holdrinet *et al.* 1978), mais récemment il a été démontré que les sédiments contaminés des tributaires continuent de contaminer le lac (Warry et Chan 1981 ; Scrudato et Delprete 1982).

L'ensemble des indications selon lesquelles la pollution par le mirex est restreinte au lac Ontario et à deux de ses tributaires (Gilbertson 1977), et n'est pas exportée vers le Saint-Laurent (Holdrinet *et al.* 1978), permet de déterminer que parmi les anguilles migratrices récoltées par la pêche commerciale entre le lac Saint-Pierre et Kamouraska en 1982, 74 % provenaient du lac Ontario. La concentration de mirex dans ces anguilles était de 0,17 ± 0,19 $\mu g \cdot g^{-1}$, semblable à celle des anguilles du lac Ontario. Dans les secteurs B et C, une anguille sur 40 et trois anguilles résidentes sur 20 respectivement contenaient du mirex (tableau 2). Le pourcentage est bas relativement aux 100 % du

TABLEAU 2. Pourcentage d'anguilles contaminées (migratrices et résidentes) et concentration du mirex par secteur : A— lac Ontario et tronçon Kingston–Cornwall ; B— lac Champlain et rivière Richelieu ; C— lac Saint-Pierre, Québec et Kamouraska. (La taille de l'échantillon figure entre parenthèses.)

Secteur	Statut (nombre)	% d'anguilles contaminées (nombre)	Concentration moyenne du mirex dans les anguilles contaminées ($\mu g \cdot g^{-1}$)
A	Migratrices (10)	100 (10)	0,14±0,06
	Résidentes (40)	100 (40)	0,19±0,12
B	Migratrices (39)	3 (1)	0,004
	Résidentes (1)	0 (0)	—
C	Migratrices (342)	74 (253)	0,17±0,19
	Résidentes (20)	15 (3)	0,12±0,16

secteur A. Les anguilles de la Côte-Nord et des Maritimes (32 bassins) ne contenaient pas de mirex (Desjardins *et al.* 1983). Il est possible que les anguilles résidentes du lac Saint-Pierre contenant du mirex aient dévalé du lac Ontario vers le lac Saint-Pierre sans être en voie de maturation sexuelle (diamètre des oocytes : 68, 71 et 74 µm).

Les produits chimiques de synthèse stables et insolubles dans l'eau se prêtent donc bien à la discrimination des stocks de poissons, dans la mesure où, tel le mirex : (i) leur distribution dans l'environnement est connue et hétérogène (Gilbertson 1977; Kaiser 1978; Holdrinet *et al.* 1978); (ii) ils sont persistants dans l'environnement (Van Valin *et al.* 1968); (iii) ils sont transmis par la chaîne alimentaire aux poissons (Kokylinski et Livingston 1975) qui les retiennent (Insalaco *et al.* 1982) et les concentrent (Lowe *et al.* 1971). La détermination du stock dont est issu un individu sera plus ou moins précise selon que ces conditions de base sont plus ou moins réalisées. Puisque les produits chimiques de synthèse ne sont pas présents dans l'environnement à l'état naturel, l'analyse est basée sur un critère de présence–absence du contaminant. Le diagnostique est donc rapide. Par contre, les méthodes basées sur les concentrations de produits chimiques naturels tels les métaux lourds (Moreau et Barbeau 1982) sont limitées par le bruit de fond que constitue la présence naturelle généralisée de ces produits chimiques dans l'environnement. Le potentiel de résolution est moindre et la méthode est limitée aux cas les plus marqués. Le diagnostique est plus lent car il requiert un ensemble de mesures précises de plusieurs variables.

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Estimating the Population Dynamics of Coho Salmon (*Oncorhynchus kisutch*) Using Pooled Time-Series and Cross-Sectional Data

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The population dynamics of natural and hatchery coho salmon (*Oncorhynchus kisutch*) were estimated for three regions, (1) Washington coastal, (2) Columbia River region, and (3) Oregon/California coastal, using pooled time-series and cross-sectional data. Two functional forms were compared: the Beverton–Holt and Ricker models. Both models yielded very similar results. In both cases, we found that the natural coho stock recruitment is significantly affected by parent stock level (positive), parent stock density (negative), river flow (positive), and hatchery smolt release (negative). The significant factors affecting hatchery coho salmon were smolt release level (positive), smolt release density (negative), and upwelling (positive).

On a déterminé la dynamique de populations de saumons cohos (*Oncorhynchus kisutch*) sauvages et de saumons cohos élevés en piscifacture dans trois régions, (1) le littoral de l'État de Washington, (2) la région du fleuve Columbia et (3) le littoral de l'Orégon et de la California, à l'aide de séries chronologiques et de données transversales groupées. Une comparaison des modèles de Beverton–Holt et de Ricker a donné des résultats très semblables. Dans les deux cas, les auteurs ont découvert que le recrutement du stock de cohos sauvages est touché de façon significative par l'abondance du stock parental (positif), la densité du stock parental (négatif), le débit (positif) et les lâchers de saumoneaux élevés en piscifacture (négatif). Le taux de lâchers de saumoneaux (positif), la densité des saumoneaux au lâcher (négatif) et les remontées d'eau profonde (positif) sont les principaux facteurs influant sur les saumons cohos provenant de piscifactures.

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The procedures involved in managing salmon stocks have become increasingly complicated since the passage of the U.S. Fishery Conservation and Management Act in 1976. In earlier periods of stock management, decisions were often made by "feel" and on casual observation of abundance by field biologists. Today, managers have been made accountable for not only specific decisions, but also for the decision procedure. Thus, critical management decisions often hinge on alternative models of population dynamics, supplemented by the "feel" of the modellers regarding reliability of the forecasts.

There is significant controversy among biologists as to the factors that influence salmon population dynamics. Hypotheses for coho salmon (*Oncorhynchus kisutch*) population dynamics include population density (McGie 1981; Oregon Department of Fish and Wildlife (ODFW) 1982; McCarl and Rettig 1983), environmental factors such as upwelling and runoff (Favorite and Laevastu 1979), upwelling (ODFW 1982), instream competition between hatchery and wild stocks (Solazzi et al. 1983), instream competition between other salmonid species (Nickelson 1981; Stein et al. 1972), and time, size, and location of hatchery smolt release (ODFW 1982; Johnson 1982).

The most important influences on wild salmon recruitment a priori are parent stock, population density, competition from hatchery smolts, and environmental factors (upwelling and river flow). Research by Stein et al. (1972) indicates that the interaction between coho and chinook (*Oncorhynchus tshawytscha*) is minimal because of differences in life history. Other studies suggest that there is no detrimental interaction between coho and steelhead trout (*Salmo gairdneri*) stocks because of behavioral differences (Hartman 1965). Therefore, species other than coho were not included in our estimation. The timing and location of hatchery smolts may affect survival, but since data are extremely limited, we did not incorporate these factors in our study.

Currently, the role of environmental factors relative to the role of parent stock and hatchery release density is unresolved. Some research indicates that density is the single most important factor (ODFW 1982, appendix 2). Other research suggests that there is no density effect and that return of adult salmon is dependent primarily on environmental factors (ODFW 1982, appendix 3). The aforementioned research results have been based upon partial analysis. For example, in appendix 2 of the *Coho Salmon Plan* (ODFW 1982), statistical relationships for wild coho are estimated using derived data (i.e. the dependent variable parent stock is derived assuming that it is directly proportional to catch for the 1950s and 1960s). Variables such as upwelling, river flow, and hatchery smolt release were not included in this analysis. The derived data lead to errors in observations and misspecification of the model which clearly results in biased and inconsistent estimates of the parameters of population dynamics. Similar problems exist in the statistical analysis in appendix 3 (ODFW 1982). In addition, both studies in the *Coho Salmon Plan* (ODFW 1982) aggregated Columbia River and Oregon coastal stocks which have significantly different environmental characteristics. There is no clear reason to expect the parameters of the two systems to be the same.

A more comprehensive approach to the estimation of population dynamics should consider both environmental and density effects. The purpose of this study is to estimate the role of parent stock density, competition from wild/hatchery populations, and environmental factors on the population dynamics of the hatchery/wild stocks of coho salmon using pooled time-series and cross-sectional data. A comparison is made of different functional forms of the relationship. The analysis only uses data from years for which a full set of observations is available. This leads to a relatively short time-series (1966–81); however, the data are disaggregated into three distinct stocks (cross-sections), (1) Washington coastal, (2) Columbia River, and (3) Oregon/California coastal, which makes possible the use of pooled estimation. By pooled estimation we mean that the parameters developed from the time-series for each cross-section can be estimated simultaneously. This three-way disaggregation is the maximum possible given current data constraints, but this still facilitates grouping of the regional stocks by environmental conditions which are homogenous. The Washington coastal rivers tend to empty into bays and not directly into the ocean. The Columbia River is fed primarily from inland rivers, has a more regulated flow, does not empty into a bay, and is dominated by hatchery stocks. The Oregon/California rivers in which coho spawn tend to be free flowing, influenced by coastal rains, and do not typically flow into bays.

Methods

Two functional forms of the model for stock–recruitment are evaluated in this research: the Ricker (1954, 1975) and the Beverton–Holt (1957). Both are discrete time models which express recruitment at time t, R_i, as a function of parent stock in time $t - n$, P_{t-n}, where n is the number of years to maturity. The Ricker relationship is

$$(1) \quad R_t = P_{t-n} e^{\alpha + \beta P_{t-n}}.$$

The Beverton–Holt relationship is

$$(2) \quad R_t = \frac{1}{\beta + \alpha / P_{t-n}}.$$

Before the above relationships can be estimated by linear techniques, transformation of equations 1 and 2 is needed. Dividing equation 1 by P_{t-n} and taking the logarithm of both side results in a linear estimable form:

$$(3) \quad \ln \frac{R_t}{P_{t-n}} = \alpha + \beta P_{t-n}.$$

The Beverton–Holt equation 2 can be transformed by inverting both sides and multiplying by P_{t-n} to get

$$(4) \quad \frac{P_{t-n}}{R_t} = \alpha + \beta P_{t-n}.$$

Note that the transformations result in different assumptions about the stochastic effect; for the Ricker model the distribution of the error is lognormal and for the Beverton–Holt the result is varying carrying capacity.

Returning coho spawners are composed of 3-yr-old adults and 2-yr-old jacks (male) and grilse (female). The 2-yr-olds were not counted in the parent stock, since they are mostly males (females are the limiting group), and they tend to be dominated in breeding by the 3-yr-olds. The parent stock is, thus, P_{t-3} for the recruitment R_t.

In addition to parent stock, another potentially important factor determining recruits may be hatchery smolts of the same cohort (natural recruitment in t may be influenced by smolt release in $t - 1$). The other factors are ocean upwelling and river flow. Ocean upwelling is the "movement of deep, nutrient-rich water to the surface, which when exposed to sunlight and warmed, results in increased food production" (ODFW 1982, p. IID-2). We hypothesized that upwelling in $t - 1$ impacts recruitment in t. We also suspected that river flow ($t - 1$) at the time of hatchery smolt release may affect hatchery recruitment (t), and that river flow ($t - 2$) in the first year of wild smolt development may affect wild recruitment, t. We assumed that these factors entered the transformed equations 3 and 4 in a linear fashion.

The transformed Ricker equation to be estimated for the wild populations of coho is

$$(5) \quad \ln \frac{\mathrm{RN}_t}{P_{t-3}} = \alpha_N + \beta_{N1} P_{t-3} + \beta_{N2} \mathrm{SA}_{t-1} + \beta_{N3} \mathrm{SAP}_{t-1} + \beta_{N4} F_{t-2} + \beta_{N5} U_{t-1} + \epsilon_N$$

and for the hatchery stocks is

$$(6) \quad \ln \frac{\mathrm{RH}_t}{\mathrm{SA}_{t-1}} = \alpha_H + \beta_{H1} P_{t-3} + \beta_{H2} \mathrm{SA}_{t-1} + \beta_{H3} \mathrm{SAP}_{t-1} + \beta_{H4} F_{t-1} + \beta_{H5} U_{t-1} + \epsilon_H$$

where

RN_t = recruitment of natural coho in t (10^3 fish)
RH_t = recruitment of hatchery coho in t (10^3 fish)
P_{t-3} = parent stock of coho in $t - 3$ (10^3 fish)
SA_{t-1} = hatchery smolts released in $t - 1$ (10^3 kg)
SAP_{t-1} = private releases of coho smolts (10^3 kg)
F_{t-2} = river flow index, $t - 2$ (discharge (m^2/s) of selected rivers divided by the average flow)
F_{t-1} = river flow index, $t - 1$ (same as above)
U_{t-1} = upwelling index ($t - 1$)
α, β_i = parameters to be estimated
ϵ = error term.

The Beverton–Holt equation for the wild stocks is

$$(7) \quad \frac{P_{t-3}}{\mathrm{RN}_t} = \alpha_N + \beta_{N1} P_{t-3} + \beta_{N2} \mathrm{SA}_{t-1} + \beta_{N3} \mathrm{SAP}_{t-1} + \beta_{N4} F_{t-2} + \beta_{N5} U_{t-1} + \epsilon_N$$

and for the hatchery stocks is

$$(8)\quad \frac{\mathrm{SA}_{t-1}}{\mathrm{RH}_t} = \alpha_H + \beta_{H1} P_{t-3} + \beta_{H2}\mathrm{SA}_{t-1} + \beta_{H3}\mathrm{SAP}_{t-1} + \beta_{H4} F_{t-1} + \beta_{H5} U_{t-1} + \epsilon_H.$$

The data used in the estimation were obtained from the Oregon Department of Fisheries and Wildlife and the Washington Department of Fisheries, and are available from the authors on request. Recruitment for a given year is total stock composed of commercial ocean troll catch, ocean sport catch, net catch (if applicable), natural spawning escapement, and hatchery returns. The portions of the recruitment resulting from hatchery smolts are determined by the ratio of on-station plus off-station hatchery returns to total escapement times total stock. The portion attributed to the naturally breeding population is the remainder of total stock. In the first phase of this work, we made an attempt to determine what proportion of the ocean catch in one area was derived from another area's stocks (e.g. the part of the Oregon/California ocean catch that comes from Columbia stocks and Washington stocks, etc.), but tag data that would allow this type of disaggregation were found to be too spotty and localized to be useful.

The parent stock of natural coho, P_{t-3}, was determined by the sum of the estimated natural escapement and the off-station returns of hatchery stock. The hatchery smolt releases, S_{t-1}, were measured by weight.

The river flow index was computed by dividing that discharge (m^2/s) of selected rivers from October–September in each region by the average river flow over the observed time period (United States Geological Survey, various years). An average of the river indexes for each region was calculated. In Washington, the flow of the Chehalis River at Porter (No. 12031000) was used; for the Columbia region, the flow of the Columbia River at The Dallas (No. 14105700) and the Willamette at Salem (No. 14191000) were used; and for Oregon/California, the flow of the Umpqua River near Elkton (No. 14321000) and the Klamath River near Klamath Falls (No. 11530500) were used. The upwelling index was found in the *Coho Management Plan* (ODFW 1982). The index increases with upwelling.

The existence of a 3-yr lag in wild parent stock reduces the total number of observations in each of the three cross-sections (regional stocks) to 13. Given that our objective is to obtain estimates of six parameters per cross-section, the small number of observations per cross-section creates a degree of freedom problem. However, if some of the parameters are restricted to be equal between cross-sections, the problem is substantially reduced.

The decision to undertake a pooled estimate from the time-series and cross-sectional data depends on whether or not the parameters in question may be inferred to be equal between cross-sections. The procedure test for equality between cross-sections is to pool all the data and regress the entire set of data as follows (Maddala 1977):

$$\begin{bmatrix} Y_1 \\ Y_2 \\ \cdot \\ \cdot \\ \cdot \\ Y_N \end{bmatrix} = \alpha_1 \begin{bmatrix} 1 \\ 0 \\ \cdot \\ \cdot \\ \cdot \\ 0 \end{bmatrix} + \alpha_2 \begin{bmatrix} 0 \\ 1 \\ \cdot \\ \cdot \\ \cdot \\ 0 \end{bmatrix} + \ldots + \alpha_N \begin{bmatrix} 0 \\ 0 \\ \cdot \\ \cdot \\ \cdot \\ 1 \end{bmatrix} + \beta_1 \begin{bmatrix} X_1 \\ 0 \\ \cdot \\ \cdot \\ \cdot \\ 0 \end{bmatrix} + \beta_2 \begin{bmatrix} 0 \\ X_2 \\ \cdot \\ \cdot \\ \cdot \\ 0 \end{bmatrix} + \ldots + \beta_N \begin{bmatrix} 0 \\ 0 \\ \cdot \\ \cdot \\ \cdot \\ X_N \end{bmatrix} + \begin{bmatrix} u_1 \\ u_2 \\ \cdot \\ \cdot \\ \cdot \\ u_N \end{bmatrix}$$

where Y_i is a vector of independent variable observation in cross-section i, X_i is a vector of dependent variable observation in cross-section i, and $i = 1, \ldots, N$.

The hypotheses to be tested are

$$H_1\colon\ \alpha_1 = \alpha_2 = \ldots = \alpha_N,$$
$$\beta_1 = \beta_2 = \ldots = \beta_N$$
$$H_2\colon\ \alpha_1 = \alpha_2 = \ldots = \alpha_N$$
$$H_3\colon\ \beta_1 = \beta_2 = \ldots = \beta_N.$$

The first hypothesis is equivalent to requiring $2N - 2$ linear restrictions:

$$\alpha_1 = \alpha_N, \alpha_2 = \alpha_N, \ldots, \alpha_{N-1} = \alpha_N$$
$$\beta_1 = \beta_N, \beta_2 = \beta_N, \ldots, \beta_{N-1} = \beta_N.$$

This requires an F test for H_1 given by

$$F = \frac{(S_2 - S_1)/(2N - 2)}{S_1 \Big/ \left(\sum_i t_i - 2N\right)}$$

where

S_1 = unrestricted residual sum of squares

S_2 = restricted residual sum of squares

t_i = number of observations in cross-section i

N = number of cross-sections

$(2N - 2)$ = number of linear restrictions

$\sum_i t_i - 2N$ = degrees of freedom.

For the hypotheses H_2 and H_3, the number of restrictions is $(N - 1)$. If the F ratio is not significant (i.e. one cannot reject the hypothesis that the coefficients are equal), the parameter estimates can be pooled.

An iterative process can be used to decide which coefficients are appropriate for pooling, requiring additional conditional tests. For example, if the F statistic on H_2 is very low, and it is decided to pool the intercepts but not the slopes, a conditional test is necessary:

$$H_4\colon\ \beta_1 = \beta_2 = \ldots = \beta_N \quad \text{given } \alpha_1 = \alpha_2 = \ldots = \alpha_N.$$

The F test is then again used.

TABLE 1. Ricker relationship for natural coho stocks corrected for autocorrelation. Dependent variable: log (RN_t/P_{t-3}). Level of significance: *0.05, **0.01.

Variable[a]	Coefficient		*t*-statistic	
A_1	α_1	3.08**	4.56	Observation = 39
A_2	α_2	0.95	0.86	$\hat{\rho} = 0.397$**
A_3	α_3	2.53**	2.68	Asymptotic *t*-statistic = 2.69
$P_{t-3,1}$	β_{11}	−0.0173**	−3.23	$R^2 = 0.72$
$P_{t-3,2}$	β_{12}	−0.0248*	−2.44	Adjusted $R^2 = 0.55$
$P_{t-3,3}$	β_{13}	−0.0035**	−2.57	
$SA_{t-1,1}$	β_{21}	−0.0019	−0.89	
$SA_{t-1,2}$	β_{22}	0.0010	0.91	
$SA_{t-1,3}$	β_{23}	−0.0035	−0.68	
$SAP_{t-1,3}$	β_{33}	−0.0071	−0.61	
$F_{t-2,1}$	β_{24}	0.518	1.42	
$F_{t-2,2}$	β_{42}	0.320	0.68	
$F_{t-2,3}$	β_{43}	0.363	1.01	
$U_{t-1,1}$	β_{51}	−0.00028	−0.17	
$U_{t-1,2}$	β_{52}	0.00071	0.36	
$U_{t-1,3}$	β_{53}	0.00016	0.094	

H_1:	$\alpha_1 = \alpha_2 = \alpha_3;\ \beta_{i1} = \beta_{i2} = \beta_{i3}$ $i = 1, 2, \ldots, 5$		$F_{11,23}$	2.08
H_2:	$\alpha_1 = \alpha_2 = \alpha_3$		$F_{2,23}$	1.35
H_3:	$\beta_{11} = \beta_{12} = \beta_{13}$		$F_{2,23}$	5.11*
H_4:	$\beta_{21} = \beta_{22} = \beta_{23} = \beta_{33}$		$F_{3,23}$	0.76
H_5:	$\beta_{41} = \beta_{42} = \beta_{43}$		$F_{2,23}$	1.53
H_6:	$\beta_{51} = \beta_{52} = \beta_{53}$		$F_{2,23}$	0.07
Conditional tests on the Ricker relationship for natural coho stocks (pooled estimation)[b]				
H_7:	$\alpha_1 = \alpha_2 = \alpha_3$	given H_4, H_5, H_6 hold	$F_{2,30}$	2.44
H_8:	$\beta_{11} = \beta_{12} = \beta_{13}$	given H_4, H_5, H_6 hold	$F_{2,30}$	5.46**
H_9:	$\beta_{21} = \beta_{22} = \beta_{23} = \beta_{33}$	given H_2, H_5, H_6 hold	$F_{3,29}$	1.32
H_{10}:	$\beta_{11} = \beta_{12} = \beta_{13}$	given H_2, H_5, H_6 hold	$F_{2,30}$	5.32**
H_{11}:	$\beta_{41} = \beta_{42} = \beta_{43}$	given H_2, H_4, H_6 hold	$F_{2,30}$	2.39
H_{12}:	$\beta_{11} = \beta_{12} = \beta_{13}$	given H_2, H_4, H_6 hold	$F_{2,30}$	4.47*
H_{13}:	$\beta_{51} = \beta_{52} = \beta_{53}$	given H_2, H_4, H_5 hold	$F_{2,30}$	1.18
H_{14}:	$\beta_{11} = \beta_{12} = \beta_{13}$	given H_2, H_4, H_5 hold	$F_{2,30}$	3.46*

[a] Subscripts: 1, Washington coastal; 2, Columbia River; 3, Oregon/California coastal.
[b] Several estimations were necessary to derive the statistics above.

The use of time-series data generally results in autocorrelated errors, leading to least squares estimates which are unbiased and consistent, but not efficient (not minimum variance).[1] When cross-sectional data are used, heteroskedasticity often results; that is, the variance in the error term differs between cross-sections. In addition, there may be correlation between the cross-sections, particularly to be expected with salmon stocks, since they are continuous over a range of coastline. As with autocorrelation, the ordinary least squares estimates under these conditions are unbiased, but not efficient. The estimated variances with autocorrelation and heteroskedasticity are, therefore, biased and result in invalid *t* and *F* statistics (Intriligator 1978).

The pooled estimation was corrected for autocorrelation in the time-series and heteroskedasticity and correlation between the cross-sections. The procedure used is found in Kmenta (1971, p. 512–514) and briefly summarized in the Appendix.

Results of Estimation

Tables 1 and 2 contain estimates of the parameters of the Ricker model for natural (Table 1) and hatchery (Table 2) stocks. The estimation was corrected for first-order autocorrelation, but not heteroskedasticity in these first tests because there are too few degrees of freedom. The test for equality of all cross-sectional (regional) coefficients (hypothesis H_1) cannot be rejected at the 0.05 level. However, a priori one might expect the own stock density effect to differ between the regions due to differing carrying capacities. Therefore, conditional tests were done to see if the coefficients associated with the regional parental stocks (in the case of natural coho) and smolt release (in the case of hatchery coho) were equivalent. In general, the conditional hypotheses of cross-sectional (regional) equality associated with the variables above, H_7–H_{14} in Tables 1 and 2 can often be rejected or nearly rejected at the 0.05 level.

From the hypothesis tests performed in the first estimation procedure, decisions were made as to which cross-sectional (regional) parameter estimates could be restricted to be equal. In

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[1] Since parent stock is derived from recruitment, in the presence of autocorrelation, parent stock will be correlated with the error. This will lead to another source of bias and inconsistency. Consistent estimates can be obtained by the method of instrumental variables (Intriligator 1978). However, it is difficult to find an instrumental variable for parent stock, and it is unclear, with small samples, whether this method would improve the estimates. Therefore, it is assumed that the correlation between parent stock and the error is zero. The properties of the estimates could be further evaluated using Monte Carlo simulations; however, this is beyond the scope of this research.

TABLE 2. Ricker relationship for hatchery coho stocks corrected for autocorrelation. Dependent variable: log $(\mathrm{RH}_t/\mathrm{SA}_{t-1})$. Level of significance: *0.05, **0.01.

Variable[a]	Coefficient	t-statistic	
A_1	1.16	0.35	Observation = 39
A_2	0.98	0.17	$\hat{\rho} = -0.568^{**}$
A_3	−3.52*	−2.01	Asymptotic t-statistic = −4.31
$P_{t-3,1}$	0.0088	1.15	$R^2 = 0.70$
$P_{t-3,2}$	0.014	1.15	Adjusted $R^2 = 0.50$
$P_{t-3,3}$	0.0029*[b]	1.75	
$\mathrm{SA}_{t-1,1}$	−0.0057**	−2.87	
$\mathrm{SA}_{t-1,2}$	−0.0022**	−2.50	
$\mathrm{SA}_{t-1,3}$	0.00023	0.20	
$\mathrm{SAP}_{t-1,3}$	0.0035*	2.18	
$F_{t-1,1}$	−0.066	−0.11	
$F_{t-1,2}$	−0.132	−0.22	
$F_{t-1,3}$	0.223	0.64	
$U_{t-1,1}$	−0.00061	−0.22	
$U_{t-1,2}$	0.0017	0.85	
$U_{t-1,3}$	0.0024	1.11	

H_1:	$\alpha_1 = \alpha_2 = \alpha_3;\ \beta_{i1} = \beta_{i2} = \beta_{i3}$		$F_{11,23}$	1.74
H_2:	$\alpha_1 = \alpha_2 = \alpha_3$		$F_{2,23}$	1.89
H_3:	$\beta_{11} = \beta_{12} = \beta_{13}$		$F_{2,23}$	0.68
H_4:	$\beta_{21} = \beta_{22} = \beta_{23}$		$F_{2,23}$	1.55
H_5:	$\beta_{41} = \beta_{42} = \beta_{43}$		$F_{2,23}$	0.18
H_6:	$\beta_{51} = \beta_{52} = \beta_{53}$		$F_{2,23}$	0.39

Conditional test on the Ricker relationship for hatchery stocks (pooled estimation)[c]

H_7:	$\alpha_1 = \alpha_2 = \alpha_3$	given H_3, H_4, H_7 hold	$F_{2,29}$	2.83
H_8:	$\beta_{21} = \beta_{22} = \beta_{23}$	given H_3, H_6, H_7 hold	$F_{2,29}$	1.47
H_9:	$\beta_{11} = \beta_{12} = \beta_{13}$	given H_2, H_6, H_7 hold	$F_{2,29}$	1.45
H_{10}:	$\beta_{21} = \beta_{22} = \beta_{23}$	given H_2, H_6, H_7 hold	$F_{2,29}$	3.89*
H_{11}:	$\beta_{41} = \beta_{42} = \beta_{43}$	given H_2, H_3, H_7 hold	$F_{2,29}$	0.43
H_{12}:	$\beta_{21} = \beta_{22} = \beta_{23}$	given H_2, H_3, H_7 hold	$F_{2,29}$	2.30
H_{13}:	$\beta_{51} = \beta_{52} = \beta_{53}$	given H_2, H_3, H_6 hold	$F_{2,29}$	0.49
H_{14}:	$\beta_{21} = \beta_{22} = \beta_{23}$	given H_2, H_3, H_6 hold	$F_{2,29}$	2.65

[a] Subscripts: 1, Washington coastal; 2, Columbia River; 3, Oregon/California coastal.

[b] The unexpected significance of the coefficient associated with $P_{t-3,3}$ may result because of the large number of parameters being estimated relative to the number of observations and because in region 3 (California/Oregon coastal area) the hatchery releases are diffused over the region and are comparatively low.

[c] Several estimations were necessary to derive the statistics above.

general, it seemed appropriate to restrict the intercept and parameters on the environmental variables. The desirability of restricting the parameters on population density was ambiguous. Therefore, three final forms are presented.

Three final forms chosen for the Ricker model are given in Table 3. All these estimations were corrected for autocorrelation in the time-series, heteroskedasticity in the cross-sections, and correlation between cross-sections as previously described. The first in both tables is the case where the coefficients for regional parent stock (natural) and smolt release (hatchery) are estimated separately, but all other variables are pooled. The second pools all variables and the final equation is one where the environmental variables and the variable for natural parent stock/smolts release are not included for the hatchery/natural case. The three analogous equations were also estimated for the Beverton–Holt model. Results appear in Table 4.

Both models yield similar results. The coefficients of the natural population dynamics equations have the expected sign on the constant term and parent stock. The results imply that increased parent stock tends to increase recruitment and that increased parent stock density tends to reduce recruitment. The estimated coefficient on hatchery smolt release indicates that smolt release negatively affects natural recruitment as expected. The sign on river flow is positive, implying that increased flow increases recruitment. This seems reasonable, since greater river flow provides more area and oxygenation. The estimated results do not substantiate the hypothesis that upwelling is an important environmental factor affecting natural salmon stocks. The most significant variables in all the natural coho models are the intercept and the parent stock. The second model, with all the coefficients restricted, indicates that smolt release may strongly influence natural recruitment in a negative fashion.

For the hatchery stock model, the coefficients on smolt release tend to be the most significant and are of the expected sign. They indicate that a density effect is important. The coefficients associated with natural parent stock and private smolt release (competing populations) sometimes have an unexpected sign and are, in all cases, insignificant at the 0.05 level. This suggests that the natural population of coho does not significantly impact the survival of smolt to adults. It also indicates that the ocean-released private aquacultured coho do not significantly compete with public hatchery releases. Thus, the density effect of hatchery smolt releases may be a result of crowding in the rivers or hatchery release points. This result may also indicate that hatcheries stocked at high density result in weaker smolts. The river flow at the year of smolt release is insignificant at the 0.05 level and appears to have a negative effect. We expected that this variable would be weak because hatchery-released smolts tend to spend relatively little time in the river. The coefficient on upwelling is significant in some equations and has a positive sign. This implies that greater upwelling may improve the survival of hatchery releases.

From the estimated parameters, equilibrium natural recruitment, maximum sustainable yield natural recruitment, and maximum sustainable yield natural spawners are derived from both models (Table 5). Maximum yield levels for hatchery recruitment and hatchery smolt release are given in Table 6.

Discussion

In this study, pooled time-series and cross-sectional data were used to estimate population dynamics for the coho salmon stocks of the Washington coastal area, the Columbia River region, and the California/Oregon coastal area. We found that for both Ricker and Beverton–Holt models that natural stock recruitment was positively affected by parent stock, negatively affected by hatchery smolt releases, and positively affected by river flow. For the hatchery stocks it was concluded that recruitment was significantly affected positively by smolt release level, negatively by smolt release density, and positively by ocean upwelling.

Recruitment depends on environmental factors and hatchery smolt release; however, the results presented in Table 6 using the Ricker model indicate that the maximum sustainable yield spawner level is around 190 000 – 200 000 coho for Washington coastal, 159 000 – 165 000 coho for Columbia River, and 180 000 – 200 000 coho for Oregon/California coastal. The PFMC escapement goals for 1983 are 75 000 coho for the Washington coastal area and 140 000 coho (200 000 coho long term) for the combined Columbia River and Oregon/California area. If it is assumed that the goal is to maximize sustainable

TABLE 3. Ricker models (pooled estimation). Level of significance: *0.05, **0.01.

1. Natural stock; dependent variable: log (RN_t/P_{t-3})

(1)1)	Variable	Constant	$P_{t-3,1}$	$P_{t-3,2}$	$P_{t-3,3}$	TSA_{t-1}[a]	F_{t-2}	U_{t-1}
	Coefficient	2.39**	−0.00720	−0.0175*	−0.00465**	−0.00084	0.478*	−0.00034
	t-statistic	(5.35)	(−1.32)	(−1.59)	(−4.12)	(−1.36)	(1.75)	(−0.26)
	$R^2 = 0.63$	Adjusted $R^2 = 0.56$			Constant $\hat{\rho} = 0.121$		Observations = 39	
	H: $\beta_{11} = \beta_{12} = \beta_{13}$				$F_{2,33} = 1.46$			
(1.2)	Variable	Constant		P_{t-3}		TSA_{t-1}[a]	F_{t-2}	U_{t-1}
	Coefficient	2.49**		−0.00411**		−0.00120**	0.390*	−0.00063
	t-statistic	(8.22)		(−5.66)		(−4.62)	(1.68)	(−0.58)
	$R^2 = 0.59$	Adjusted $R^2 = 0.54$			Constant $\hat{\rho}^b = -0.044$		Observations = 39	
(1.3)	Variable	Constant	$P_{t-3,1}$	$P_{t-3,2}$	$P_{t3,3}$			
	Coefficient	2.36**	−0.00729	−0.0290**	−0.00353**			
	t-statistic	(12.30)	(−0.31)	(−3.82)	(−4.01)			
	$R^2 = 0.54$	Adjusted $R^2 = 0.50$			Constant $\hat{\rho} = 0.136$		Observations = 39	

2. Hatchery stock; dependent variable: log (RH_t/SA_{t-1})

(2.1)	Variable	Constant	P_{t-3}	$SA_{t-1,1}$	$SA_{t-1,2}$	$SA_{t-1,3}$	$SAP_{t-1,3}$	F_{t-1}	U_{t-1}
	Coefficient	−1.19	0.0019	−0.00156	−0.00143**	−0.00930**	0.00178	−0.0364	0.0024
	t-statistic	(−0.48)	(0.82)	(−1.41)	(−3.00)	(−2.78)	(0.92)	(−0.10)	(1.49)
	$R^2 = 0.61$		Adjusted $R^2 = 0.52$			Constant $\hat{\rho} = -0.255$		Observations = 39	
	H: $\beta_{21} = \beta_{22} = \beta_{23}$				$F_{2,32} = 1.98$				
(2.2)	Variable	Constant	P_{t-3}		SA_{t-1}		$SAP_{t-1,3}$	F_{t-1}	U_{t-1}
	Coefficient	−1.43	−0.0020		−0.00104**		−0.000328	−0.123	0.00261*
	t-statistic	(−1.00)	(−1.57)		(−2.71)		(−0.21)	(−0.37)	(1.83)
	$R^2 = 0.44$		Adjusted $R^2 = 0.36$			Constant $\hat{\rho} = -0.109$		Observations = 39	
(2.3)	Variable	Constant		$SA_{t-1,1}$	$SA_{t-1,2}$	$SA_{t-1,3}$			
	Coefficient	1.36*		−0.000536**	−0.00187**	−0.00847**			
	t-statistic	(2.33)		(−3.41)	(−5.82)	(−5.22)			
	$R^2 = 0.55$		Adjusted $R^2 = 0.51$			Constant $\hat{\rho} = -0.465$		Observations = 39	

[a] Includes all public and private releases.

[b] The low estimate of $\hat{\rho}$ is indicative of minimal autocorrelation when parent stocks are pooled.

TABLE 4. Beverton–Holt models (pooled estimation). Level of significance: *0.05, **0.01.

1. Natural stock; dependent variable: (P_{t-3}/RN_t)

(1.1)	Variable	Constant	$P_{t-3,1}$	$P_{t-3,2}$	$P_{t-3,3}$	TSA_{t-1}[a]	F_{t-2}	U_{t-1}
	Coefficient	0.0712	0.00132*	0.00376*	0.000813**	0.00011	−0.0759*	0.00011
	t-statistic	(1.01)	(1.72)	(1.76)	(4.67)	(1.01)	(−1.73)	(0.52)
	$R^2 = 0.61$		Adjusted $R^2 = 0.53$		Constant $\hat{\rho} = 0.114$			
(1.2)	Variable	Constant		P_{t-3}		TSA_{t-1}[a]	F_{t-2}	U_{t-1}
	Coefficient	0.0497		0.000695**		0.000184**	−0.0646	0.000209
	t-statistic	(1.04)		(5.98)		(4.53)	(−1.65)	(1.19)
	$R^2 = 0.56$		Adjusted $R^2 = 0.51$		Constant $\hat{\rho} = -0.097$			
(1.3)	Variable	Constant	$P_{t-3,1}$	$P_{t-3,2}$	$P_{t-3,3}$			
	Coefficient	0.0745**	0.000687	0.00513**	0.000683**			
	t-statistic	(2.55)	(1.20)	(3.63)	(4.99)			
	$R^2 = 0.54$		Adjusted $R^2 = 0.50$		Constant $\hat{\rho} = 0.109$			

2. Hatchery stock; dependent variable: (SA_{t-1}/RH_t)

(2.1)	Variable	Constant	P_{t-3}	$SA_{t-1,1}$	$SA_{t-1,2}$	$SA_{t-1,3}$	$SAP_{t-1,3}$	F_{t-1}	U_{t-1}
	Coefficient	0.585	−0.000396	0.00237	0.00118**	0.0110**	−0.00304	0.281	−0.0014
	t-statistic	(0.75)	(−1.20)	(1.35)	(2.78)	(2.61)	(−1.13)	(0.79)	(−0.0034)
	$R^2 = 0.53$		Adjusted $R^2 = 0.43$		Constant $\hat{\rho} = -0.15$				
(2.2)	Variable	Constant	P_{t-3}		SA_{t-1}		$SAP_{t-1,3}$	F_{t-1}	U_{t-1}
	Coefficient	0.576	0.00187		0.00105*		0.000191	0.386	−0.0019
	t-statistic	(0.85)	(1.02)		(2.37)		(0.083)	(0.77)	(−0.033)
	$R^2 = 0.28$		Adjusted $R^2 = 0.17$		Constant $\hat{\rho} = -0.34$				
(2.3)	Variable	Constant		$SA_{t-1,1}$	$SA_{t-1,2}$	$SA_{t-1,3}$			
	Coefficient	0.156		0.00329**	0.00145**	0.00704**			
	t-statistic	(1.08)		(3.56)	(5.92)	(4.80)			
	$R^2 = 0.40$		Adjusted $R^2 = 0.35$		Constant $\hat{\rho} = -0.41$				

[a] Includes all public and private releases.

TABLE 5. Comparison of natural coho recruitment relationships: Ricker, Beverton–Holt (thousands of fish).

	Equilibrium recruitment			Maximum sustainable yield spawners			Maximum sustainable yield recruitment[b]		
	WA	CR	OR/CA	WA	CR	OR/CA	WA	CR	OR/CA
				Given mean TSA, R, U[a]					
Ricker (Table 3, Eq. 1.2)	614	419	602	199	159	197	1092 (722, 1650)	462 (305, 701)	1036 (688, 1560)
Beverton–Holt (Table 4, Eq. 1.2)	1334	1158	1324	283	355	292	1051 (835, 1417)	802 (685, 966)	1032 (829, 1368)
				Given mean R, U, and 1980 TSA					
Ricker	562	440	506	190	165	179	877 (580, 1327)	512 (337, 777)	687 (451, 1047)
Beverton–Holt	1284	1177	1236	314	352	337	975 (809, 1256)	825 (706, 991)	899 (751, 1119)
PFMC goal (1983)				75	140 (200)[c]				

[a] Mean R: 0.92 (WA), 0.92 (CR), 0.93 (OR/CA); mean U: 279 (WA), 299 (CR), 279 (OR/CA); mean TSA (10^3 kg): 131 (WA), 792 (CR), 170 (OR/CA); 1980 TSA (10^3 kg): 298 (WA), 722 (CR), 494 (OR/CA).

[b] 70% confidence interval (parentheses) calculated given maximum sustainable yield levels of spawners.

[c] Long-term goal.

TABLE 6. Maximum hatchery recruitment for the different models.

	WA	CR	OR/CA
Ricker (Table 3, Eq. 2.3)			
Smolt release (10^3 kg) for maximum recruitment	187	535	118
Maximum recruitment (10^3 fish)	267 (203, 391)[a]	762 (580, 1110)[a]	169 (129, 246)[a]
Beverton–Holt (Table 4, Eq. 2.3)			
Maximum recruits (10^3 fish)	304	690	142
Smolt release → ∞			
Mean public smolt releases (10^3 kg)	131	792	153
1981 public smolt releases (10^3 kg)	298	722	123
Maximum recruitment smolt release (10^3 kg), ODFW[b]		854	

[a] 70% confidence interval assuming maximum recruitment smolt release. Confidence intervals for the Beverton–Holt model are not given, since smolt release approaches infinity.

[b] ODFW (1982, appendix 3f, p. 7) assumes 37.5 fish/kg.

yield, the results of this model suggest that these escapement values are too low. Of course, maximum sustainable yield may not necessarily be an optimal goal once economic and political considerations are taken into account. This, however, is beyond the scope of this paper.

The ODFW (1982) indicated that the maximum recruitment smolt release for hatcheries is approximately 854 (10^3 kg) for the Columbia River and Oregon coast. Our estimates suggest that the maximum recruitment smolt release is lower, at about 535 (10^3 kg) for the Columbia River and 118 (10^3 kg) for the Oregon/California coast (see Table 6). The Columbia River releases exceed this amount by a significant margin. The current Oregon/California coastal public releases appear to be near the maximum level. The public Washington coastal smolt releases are significantly beyond the maximum level. Here again, the maximum level is not necessarily the optimum level given economic and political considerations. It should also be realized that these estimates are dependent on current hatchery practices and the current number of hatcheries. This model is useful for considering an increase in releases from current facilities rather than an increase in releases resulting from a new facility.

Finally, a fruitful area of further research would be to use these estimation methods with an increased number of cross-sections (regional salmon stocks), either through additional disaggregation or by including more areas along the Pacific coast. In addition, improved proxies for environmental factors should improve the estimates.

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Appendix

The characteristics of the disturbances of the untransformed model (Kmenta 1971) are:

$$E(\epsilon_{it}^2) = \sigma_{it} \quad \text{(heteroskedasticity)}$$

$$E(\epsilon_{it}\epsilon_{jt}) = \sigma_{ij} \quad \text{(correlation between cross-sections)}$$

$$\epsilon_{it} = \rho_i \epsilon_{i,t-1} + u_{it} \quad \text{(first-order autoregression)}$$

where

$$u_{it} \sim N(0, \phi_{ii})$$

$$E(\epsilon_{i,t-1}, u_{jt}) = 0$$

$$E(u_{it} u_{jt}) = \phi_{ij}$$

$$E(u_{it} u_{js}) = 0 \quad (t \neq s)$$

$$i, j = 1, 2, \ldots, N.$$

The initial value of ϵ is assumed to have the following characteristics:

$$\epsilon_{io} \sim N\left(0, \frac{\phi_{ii}}{1 - \rho_i^2}\right)$$

$$E(\epsilon_{io}, \epsilon_{jo}) = \frac{\phi_{ij}}{1 - \rho_i \rho_j}.$$

The matrix Ω for generalized least squares estimation is

$$\Omega = \begin{bmatrix} \sigma_{11}P_{11} & \sigma_{12}P_{12} & \cdots & \sigma_{1N}P_{1N} \\ \sigma_{21}P_{21} & \sigma_{22}P_{22} & \cdots & \sigma_{2N}P_{2N} \\ \vdots & \vdots & & \vdots \\ \sigma_{N1}P_{N1} & \sigma_{N2}P_{N2} & \cdots & \sigma_{NN}P_{NN} \end{bmatrix}$$

where

$$P_{ij} = \begin{bmatrix} 1 & \rho_j & \rho_j^2 & \cdots & \rho_j^{T-1} \\ \rho_i & 1 & \rho_j & \cdots & \rho_j^{T-2} \\ \rho_i^2 & \rho_i & 1 & \cdots & \\ \vdots & \vdots & \vdots & & \vdots \\ \rho_i^{T-1} & \rho_i^{T-2} & \rho_i^{T-3} & \cdots & 1 \end{bmatrix}.$$

Consistent estimates of Ω are found by applying ordinary least squares to all the pooled observations and calculating the residuals, e_{it}. The residuals e_{it} are used to calculate estimates of ρ_i by the formula

$$\hat{\rho}_i = \frac{\Sigma\, e_{it} e_{i,t-1}}{\Sigma\, e_{i,t-1}^2}.$$

The $\hat{\rho}_i$ are used to transform the data as follows:

$$Y_{it}^* = Y_{it}^* - \hat{\rho}_i Y_{i,t-1}^*$$

$$X_{it,k}^* = X_{it,k}^* - \hat{\rho}_i X_{i,t-1,k}^*$$

$$t = 2, 3, \ldots, T$$

$$i = 1, 2, \ldots, N$$

$$k = 1, 2, \ldots, K \quad \text{(number of variables).}$$

The fransformed equation is

$$Y_{it}^* = \beta_1 X_{it,1}^* + \beta_2 X_{it,2}^* + \ldots + \beta_K X_{it,K}^* + u_{it}^*$$

where

$$u_{it}^* = \epsilon_{it} - \hat{\rho}_i \epsilon_{i,t-1}.$$

This equation is estimated with ordinary least squares and the residuals u_{it} are calculated. The variances and covariances of the ϵ_{ij} are estimated by

$$\hat{S}_{ij} = \frac{\hat{\phi}_{ij}}{1 - \hat{\rho}_i \hat{\rho}_j}$$

where

$$\hat{\phi}_{ij} = \frac{1}{T - K - 1} \sum_{t=2}^{T} \hat{u}_{it}^* \hat{u}_{jt}^*.$$

The procedure gives consistent estimates of ρ_i, σ_{ij}, and Ω. Asymptotically efficient estimates of the coefficient matrix are given by the generalized least squares estimator

$$\tilde{\beta} = (X'\hat{\Omega}^{-1}X)^{-1}(X'\hat{\Omega}^{-1}Y)$$

with

$$\text{Asymptotic Var-Cov } (\tilde{\beta}) = (X'\hat{\Omega}^{-1}X)^{-1}.$$

The consistent estimator of $\hat{S}^2$ is given by

$$\hat{S}^2 = \frac{1}{\sum_i T_i - K - 1} \hat{u}^{*\prime}\hat{\Omega}^{-1}\hat{u}^*$$

where $\hat{u}^*$ is the vector of transformed residuals. This formula, along with the estimate of covariance matrix, can be used in F and t tests. For example:

$$F_{m,\Sigma T_i - K - 1} = \frac{(C\beta - C\beta_0)'(X'\hat{\Omega}^{-1}X)^{-1}(C\beta - C\beta_0)}{m\hat{S}^2}.$$

Estimation of Harp Seal (*Phoca groenlandica*) Pup Production from Age Samples[1]

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Cooke, J. G. 1985. Estimation of harp seal (*Phoca groenlandica*) pup production from age samples. Can. J. Fish. Aquat. Sci. 42: 468–473.

A simple numerical example shows that previously used procedures such as the "survival index" method for estimating the pup production in populations of harp seals (*Phoca groenlandica*) from samples of aged adults are unreliable because of their poor mathematical formulation. A corrected formulation, based on a maximum likelihood criterion, performed well in simulations tests. This was applied to age data from the Northwest Atlantic harp seal stock to obtain revised pup production estimates. A method to correct for the effects of errors in ageing also performed favourably in simulation trials.

Un simple exemple numérique révèle que les méthodes utilisées antérieurement pour l'estimation de la production de jeunes dans les populations de phoques du Groenland (*Phoca groenlandica*), comme «indice de survie», à partir d'échantillons de vieux adultes sont douteuses à cause de leur expression mathématique médiocre. Une formule corrigée, basée sur un critère d'évaluation de la vraisemblance maximale, a donné de bons résultats au cours de simulations. L'auteur a appliqué cette formule aux données sur l'âge obtenues du stock de phoques du Groenland peuplant la partie nord-ouest de l'Atlantique afin d'obtenir des estimations révisées de la production de jeunes. Une méthode permettant de corriger l'incidence des erreurs de détermination de l'âge s'est aussi révélée efficace au cours de simulations.

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The "survival index" method of estimating harp seal (*Phoca groenlandica*) pup production from samples of aged animals was initially outlined by Sergeant (1971). The main form of exploitation of this species in the Northwest Atlantic has been the annual harvest of pups. The numbers killed have fluctuated over the years. Year classes born in years of low pup kill tend to have a greater representation in subsequent samples of aged animals than those born in years of high pup kill. By quantifying these differences, an estimate of pup production can be obtained, on the assumption that it remains approximately constant over a short span of years.

Previous implementations of this idea have suffered from the lack of a quantitatively rigorous formulation. After illustrating the potential consequences of this deficiency, I derive a corrected method which is first subjected to extensive simulation tests before being applied to the available age data from the Northwest Atlantic harp seal population.

Problems with Previous Methods

Sergeant (1975) described several applications of his method, which was initially based on a qualitative evaluation of year-class strengths from inspection of the age samples. These qualitative evaluations, termed "survival indices," were regressed against pup kill, and the intercept, the level of pup kill that would correspond to zero survival, was the estimate of pup production.

Benjaminsen and Øritsland (1975) and Winters (1978) used an objective criterion for the evaluation of year-class strength. They defined the survival index of a given year class in a given year as

$$(1)\quad \frac{\text{Year-class representation as a proportion of sample}}{\text{Average age-class strength as a proportion of total sample}}.$$

The denominator in this expression is designed to remove the effects of both hunting mortality (other than on pups), natural mortality, and possible age-specific sampling selectivity. The survival index from each annual sample was weighted according to the sample size and averaged over the years. These weighted averages of survival indices by year class were then regressed against the annual pup kill and the intercept taken as an estimate of pup production.

Ricker (1975) reapplied the method using a functional regression between the survival index and pup kill to allow for possible natural variability in pup production and survival rates.

An essentially equivalent method involving measurement of the ratios of adjacent year-class strengths was used by Roff and Bowen (1983) as part of an assessment of the Northwest Atlantic harp seal population, although they arbitrarily restricted the data set to two pairs of cohorts for which the pup kills differed greatly.

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[1] Based on a paper presented to a workshop on Northwest Atlantic harp and hooded seals convened by the International Council for the Exploration of the Sea, København, October 1982.

The absence of a rigorous mathematical basis for these methods has been noted by Beddington and Williams (1980) and Roff and Bowen (1983). As an example of the potential consequences of this deficiency, consider the following hypothetical example:

Suppose that the real pup production is 300 000 and that the annual kill alternates between zero and 270 000 from year to year. Under these circumstances, the survival index method ought to provide an accurate estimate of pup production because the surviving numbers vary enormously between successive year classes.

Suppose further that samples from five age groups over a period of 5 yr are used, so that a total of nine year classes are included (see Table 1). Suppose also that there is uniform selectivity by age and that the rate of natural mortality is negligible. For simplicity, let the numbers in the age samples reflect exactly the proportions of the different age groups in the population (i.e. no sampling variability). Let the sample size alternate between successive years in the ratio 320:23. This ratio is chosen to yield round numbers for the numbers by age that will then be found in each sample, as shown in Table 1.

The survival indices by year class, as calculated by the Benjaminsen–Øritsland/Winters method, are listed in Table 2. Note that the ratios of these survival indices between adjacent cohorts are generally about 2:1 whereas the true survivor ratios are 10:1. Regression of the survival indices against pup kill yields a pup production estimate of 528 800, which is nearly double the true value. Use of a functional regression as proposed by Ricker (1975) yields a slightly lower estimate of 505 000.

Whereas this example may be rather artificial in some respects, it demonstrates the importance of first constructing a sound mathematical basis for the method before proceeding with more sophisticated tests.

TABLE 1. Numbers of sampled harp seals by age and year in the hypothetical example used to test the survival index method.

Year class numbers
4 3 2 1
5
6
7
8
9

		Age groups					
		1	2	3	4	5	Totals by year:
Years	1	100	10	100	10	100	320
	2	1	10	1	10	1	23
	3	100	10	100	10	100	320
	4	1	10	1	10	1	23
	5	100	10	100	10	100	320
Totals by age:		302	50	302	50	302	

TABLE 2. Survival indices by year class calculated from the hypothetical data in Table 1 using the Benjaminsen–Øritsland (1975) formula.

Year class number	Survival index
1	1.0410
2	0.5963
3	1.3083
4	0.5963
5	1.3934
6	0.5963
7	1.3083
8	0.5963
9	1.0410

A Revised Formulation

The level of pup production that best fits any given set of age data can be defined by the usual maximum likelihood criterion. A method for finding this level is outlined below. Notation is as follows:

X_{at}	no. of animals aged a alive in the population in the year t
N_{at}	no. of animals aged a in the age sample of year t
N_t	sample size in year $t \left(= \sum_a N_{at}\right)$
N_a	total sample from age group $a \left(= \sum_t N_{at}\right)$
S_a	selectivity-cum-cumulative survival to age a
K_t	pup kill in year t

The matrix of numbers alive in the population by age and year, X, will depend upon the pup production, the pup kill, and the natural and hunting mortality (other than the pup kill). The usual simplifying assumption made when applying the survival index method is that the natural and hunting mortality rates for 1+ animals do not vary significantly from year to year (although they may vary by age). These mortality rates can thus be subsumed into the composite parameter vector S, which represents the combination of cumulative survival from age zero to each age, and the age-specific sampling selectivity. The age-specific sampling selectivity for age group a is defined as the ratio of the probability that an animal of age a will be sampled to the probability that an animal of some reference age will be sampled. These assumptions may have to be modified to take account of unusually high kills of 1- and 2-yr-olds that occur in some years.

Each element of X can thus be replaced by an expression for the pup escapement for that year class. If the pup production can be assumed to be approximately constant, then the pup escapement for the year class aged a in year t is

$$(2) \quad P - K_{t-a}.$$

The notation X_{at} is retained here for generality. the probability that a random animal sampled in year t is aged a is equal to

$$(3) \quad S_a X_{at} \Big/ \left(\sum_i S_i X_{it} \right).$$

On the assumption that the age samples are independently multinomially distributed, and conditional on the annual sample sizes, N_t, the probability of obtaining a particular matrix of numbers by age is

$$(4) \quad \prod_t \left[N_t! \prod_a \left\{ \left[S_a X_{at} \Big/ \sum_i S_i X_{it} \right]^{N_{at}} \Big/ N_{at}! \right\} \right]$$

the logarithm of which, ignoring constant terms, simplifies to

$$(5) \quad L = \sum_a \sum_t N_{at} \log\{X_{at}\} + N_a \log\{S_a\} - \sum_t N_t \log\left\{ \sum_a S_a X_{at} \right\}.$$

This expression can be regarded as the log-likelihood of X and S. Maximum likelihood estimates of these parameters are obtained by maximizing L over X and S. In this application, X satisfies (2), hence is fully determined by P alone; L is therefore to be maximized over P and S.

For a given value of P, L is maximized over S by setting the derivatives of L with respect to each component of S to zero. This implies

$$(6) \quad S_a = N_a \Big/ \sum_t \Big[N_t X_{at} \Big/ \sum_i S_i X_{it} \Big].$$

If one component of S is arbitrarily fixed, then there is a unique solution for the others. Although there is no simple closed form expression for the solution, it can easily be obtained numerically by starting with some arbitrary positive values for S (such as uniform) and successively reevaluating them according to equation (6). This algorithm converges within three to five iterations provided that P is greater than the maximum kill.

By evaluating the log-likelihood (maximized over S in the manner described) for various values of P, the log-likelihood function for P can be sketched out and its maximum located numerically or graphically. An approximate α-% confidence interval for P is given by the set of values for P for which the log-likelihood differs from the maximum value by less than half the upper α-percentile of the chi-squared distribution with one degree of freedom (Cox and Hinkley 1974).

All the simulation trials and estimations documented in the following sections were also carried out using a least-squares rather than maximum likelihood criterion for the goodness of fit. In no respect were any of the results appreciably different, which indicates that the choice of criterion is not critical provided that it is consistent.

Tests of the New Formulation

It is easily verified that the procedure just outlined correctly estimates the true pup production of 300 000 in the hypothetical example given in the previous section. The next step is to evaluate the performance of the estimator under realistic levels of sampling variability with typical levels of variation in pup kill. Clearly, the precision of the estimates will increase with increasing size of the age samples and increasing variability in pup kill.

The actual historical levels of pup kill for Northwest Atlantic harp seals for the 10-yr period 1968–77 were used (see next section for further explanation). The age data were generated by random sampling from a hypothetical population. Following Winters (1978), only age groups 2–8 yr were used. The actual sample sizes of aged animals collected in each year from large-vessel catches from these year classes and age groups were also used (Bowen 1982). These pup kills and samples sizes are listed in Table 3. To approximate to the typical sample sizes by age, the slope of the curve of log-selectivity-cum-mortality against age (apparent mortality) was taken as 0.15.

Sequences of random age samples were generated on which the estimation procedure defined in the previous section was carried out.

Since the problem essentially involves finding the x-intercept of a linear regression, the distribution of the pup production estimates is skewed to the left, and lacks a finite mean or variance. Indeed, one would expect a small but finite percentage of trials to yield a likelihood that is an increasing function of pup production with no local maximum. These correspond formally to infinite or negative pup production estimates. Hence it would not be meaningful to express the results in terms of the mean and variance of the estimates obtained. Instead, the median and extremes of 100 simulation trials were recorded. A more accurate indication of the distributions of the estimates would be obtained by conducting, say, 1000 trials in each case and recording the median along with the 95-percentiles.

TABLE 3. Northwest Atlantic harp seal pup kills during 1968–77 and sizes of aged samples from large vessel catches during 1970–79 (from Bowen 1982).

Year	Pup kill (in thousands)	Sample size (age classes 2–8 yr)
1968	161	
1969	239	
1970	221	507
1971	214	207
1972	120	95
1973	103	1212
1974	119	631
1975	144	603
1976	136	605
1977	134	486
1978		640
1979		317

The Ideal Case

The method was first tested in the case where all the assumptions are satisfied, i.e. the true pup production is exactly constant, age-specific sampling selectivity and mortality (other than the pup kill) are also constant, and all age determinations are accurate. Three values of the true pup production, 300 000, 400 000, and 500 000, were examined and the estimates recorded to the nearest 5000. The results in terms of the median and extremes are listed at the top of Table 4. As expected, the estimates are unbiassed in terms of the median but become less precise as the true pup production increases. The method discriminates well between the case of 300 000 and 400 000, but does not discriminate between 400 000 and 500 000. The distribution of the estimates when the true pup production is 300 000 is shown graphically in Fig. 1 based on 1000 trials.

Having assessed the performance of the method under ideal circumstances, the effects of various departures from the underlying assumptions were then examined in turn.

Errors in Age Determination

It is not possible to age all harp seal teeth accurately. Following Stewart and Lavigne (1979), Doubleday and Bowen (1980) quantified the degree of error by comparing multiple readings of the same teeth by different workers. They estimated a preliminary error matrix representing the proportions of teeth of a given mean age reading being allocated to the different age groups. This error matrix is based on the assumption that there is no systematic bias in the readings, and that each reader's errors are independent of the others. Hence it underestimates the true extent of errors. The matrix shows that the inter-reader standard error is roughly proportional to the mean reading, and that the proportion of correct readings declines rapidly with increasing age. This justifies the decision to exclude older teeth from the analysis.

TABLE 4. Results of simulation trials on the revised pup production estimator.

True pup production	Degree of ageing error	Correction for ageing error	Median estimate (thousands)[a]	Range of estimates (thousands)[a]
		Constant pup production		
300	0	0	300	280–320
400	0	0	405	350–480
500	0	0	505	400–800
300	1	0	315	295–340
400	1	0	420	365–525
500	1	0	520	420–940
300	2	0	330	300–355
400	2	0	445	380–575
500	2	0	560	440–960
300	1	1	300	280–325
300	2	1	310	285–340
300	1	2	295	270–315
300	2	2	300	275–325
		Fluctuating pup production		
300 (5%)[b]	0	0	300	260–390
300 (10%)[b]	0	0	300	245–450
		Declining pup production		
325–275	0	0	315	295–340
350–250	0	0	330	300–365
350–250	1	0	340	310–390
350–250	2	0	365	325–450

[a] The median and range of estimates are based on 100 trials for each set of parameters, using the historical pup kills and sample sizes listed in Table 3. All estimates are given to the nearest 5000.

[b] Mean coefficient of variation in parentheses.

Some workers routinely read each tooth several times in order to improve the accuracy of age readings (e.g. Stewart and Lavigne 1984), and it may be that the existing harp seal data base could be improved in this respect.

To investigate the effects of ageing errors on the estimates, two degrees of error were considered. In the first case, the error matrix of Doubleday and Bowen (1980) was applied to the numbers at age in the hypothetical populations to yield revised sets of numbers by apparent age which were used in the estimations. If the matrix of numbers alive in the population by age by year is X, and the error matrix for ages is Q, where Q_{ij} represents the expected proportion of animals aged j which will be read as age i, then the product QX is the matrix of numbers of seals by apparent age by year.

Given that the matrix Q underestimates the degree of error, estimations were also carried out using the square of this matrix, to simulate a situation which is twice as bad. These two degrees of error are referred to as 1 and 2, respectively, in Table 4. Zero indicates no errors in ageing.

The results in Table 4 reveal small but consistent upward biasses in the estimates, which are approximately proportional to the degree of error in ageing. The distributions of estimates when the true pup kill is 300 000 for 0, 1, and 2 degrees of ageing error are shown in Fig. 1, based on the results of 1000 trials carried out for each situation.

Doubleday and Bowen (1980) attempted to correct for the effects of ageing error by applying the inverse of the error matrix to the observed data. While it is true that this will yield transformed numbers by age with the same expectations as the expected true numbers at age in the sample, the transformed distribution is no longer a multinomial sample and cannot be assigned a probability in the usual way. Indeed, the transformed samples usually contain a number of negative values. Furthermore, such a transformation involves a considerable increase in the variance of the numbers in each age class.

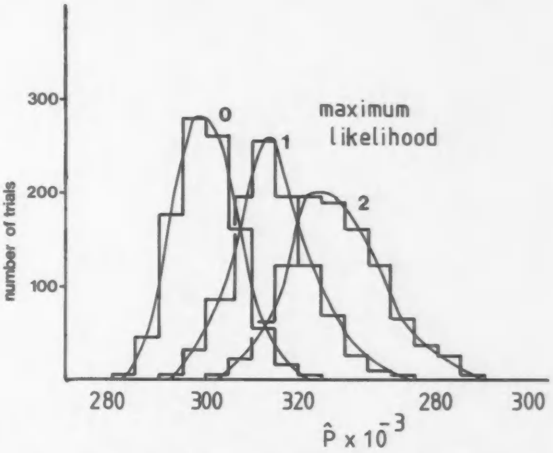

FIG. 1. Distribution of estimates of pup production (P) obtained from 100 simulation trials, with 0, 1, and 2 degrees of error in ageing (see text for explanation). The true pup production is 300 000.

The reverse method of correction is used here: the observed age samples are left unchanged, but the expected numbers by age are modified by the error matrix in the manner described prior to calculation of the likelihood. Two degrees of correction are considered: firstly, using the error matrix itself, and secondly, its square.

The results of simulation trials of this method of correcting for ageing error are shown in Table 4 for a true pup production of 300 000. They show that the method successfully removes the bias when the appropriate degree of correction is applied, without any appreciable increase in variability. As expected, undercorrection results in upward biasses in the estimates, thile overcorrection results in downward biasses.

Fluctuations in Pup Production

Since the pregnancy rate is close to 100% for mature female harp seals, the scope for annual fluctuations in pup production is limited. However, there will still be some variation: for example, when a year class from a year of high pup kill becomes mature, there will be a temporary drop in recruitment to the mature female population and hence a temporary reduction in pup production.

Trials were carried out with a mean pup production of 300 000 and coefficients of variation of 5 and 10%. As shown in Table 4, the precision of the estimates is considerably reduced. The distribution of the estimates based on 1000 trials is shown in Fig. 2 for the case of a 10% CV of pup production. The long right-hand tail of the distribution containing a few extreme overestimates is apparent.

There may also be variations in survival rates following the kill. If survival in the first year of life is density dependent (i.e. related to the density of first-year seals), then this effect will

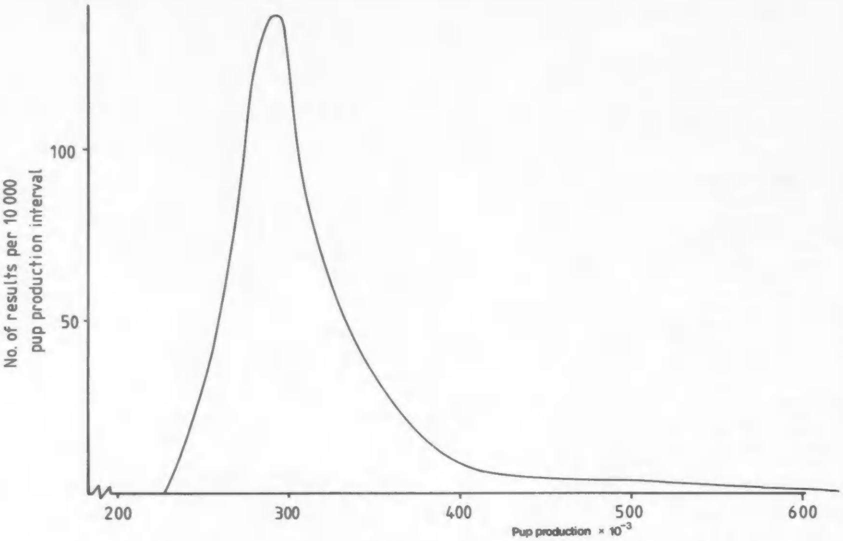

FIG. 2. Distribution of estimates of pup production obtained from 1000 simulation trials, when the true pup production fluctuates around a mean value of 300 000 with a coefficient of variation of 10%.

tend to even out the differences in year-class strengths and lead to systematic upward biasses in the estimates.

Trends in Pup Production

Since the estimates obtained in the next section indicate a decline in pup production with time, trials were carried out with a linear decline in the true pup production. Two cases were considered: a decline from 350 000 to 250 000 over the 10-yr period, and a lesser decline from 325 000 to 275 000. The results shown in Table 4 indicate that the median estimate obtained tends to be greater than the median pup production, but less than the initial pup production. The variability of the estimates is not appreciably increased.

Finally, trials were carried out showing the combined effects of ageing errors and linear declines in pup production. The biasses from these two sources are approximately additive.

Estimates of Pup Production in the Northwest Atlantic Stock of Harp Seals

Pup kill and large vessel age sample data (1961–79) were taken from Bowen (1982). Following Winters (1978), only age groups 2–8 yr were used, since the older age classes are more prone to errors in age determination, and the selectivity of the 1-yr-olds is very variable. Since at least two year classes in this age range must be represented in a year of age data for it to contribute any information, the latest year of pup production which can be estimated from these data is 1977. Pup production was estimated for the 10-yr period 1968–77 as in the simulation trials, and also for the preceding 10-yr period 1958–67.

For each 10-year period, estimates of pup production were obtained with zero, one, and two degrees of correction for ageing error, as defined in the description of the simulation trials.

TABLE 5. Estimates of pup production for the Northwest Atlantic harp seal stock using the revised estimator with age samples from large-vessel catches.

Year classes	Age samples	Ageing error correction	Estimate (thousands)[a]	95% conf. interval (thousands)[b]
1958–67	1961–74	0	502	445–620
1958–67	1961–74	1	444	400–535
1958–67	1961–74	2	410	370–480
1968–77	1971–79	0	374	374–410
1968–77	1971–79	1	336	336–365
1968–77	1971–79	2	311	311–330

[a] Best estimates given to nearest 1000.
[b] Confidence limits given to nearest 5000.

The results are listed in Table 5. Correction for ageing errors leads to approximately the same degree of reduction in the estimates as indicated by the simulation trials. The confidence intervals are consistent with the spread of the estimates obtained from the simulation trials. The estimates of pup production for the period 1968–77 are significantly lower than those for the period 1958–67 according to the confidence intervals calculated here.

Discussion

The estimates of pup production for the period 1968–77 obtained here are higher, but not significantly so, than estimates obtained by direct census in 1977 by Lavigne et al. (1980), who identified a probable downward bias in their estimate due to incomplete coverage.

These estimates of pup production for the period 1968–77 are significantly lower than estimates of production for 1978–79 obtained by Bowen and Sergeant (1983) using the method of tag–recapture. Simulation studies by Roff and Bowen (1983) showed that an increase in the population during the 1970's of sufficient magnitude to account for this discrepancy is not impossible. However, the difference in the estimates could just as easily be due to failures in the assumptions of one or both methods, and further testing of these is required before any practical conclusions can be drawn.

An analysis of the internal consistency of the age sample data would yield further information on the reliability of the estimates obtained from them. Replacement of the assumption of constant pup production in the estimation method developed in this paper with a simulation model linking pup production to the adult stock would enable identification of the range of possible population trajectories that are consistent with the age data.

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Morphological, Electrophoretic, and Fecundity Characteristics of Atlantic Snow Crab, *Chionoecetes opilio*, and Implications for Fisheries Management

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Davidson, K., J. C. Roff, and R. W. Elner. 1985. Morphological, electrophoretic, and fecundity characteristics of Atlantic snow crab, *Chionoecetes opilio*, and implications for fisheries management. Can. J. Fish. Aquat. Sci. 42: 474–482.

For adult snow crabs (*Chionoecetes opilio*), from the western Gulf of St. Lawrence, eastern and western Cape Breton Island, and eastern Newfoundland, we compared morphometric, meristic, electrophoretic, and fecundity characteristics. Our morphometric, meristic, and fecundity data indicated that snow crabs from the four areas are morphologically and biologically distinct; therefore, they represent four "phenotypic" or "biological" stocks. We propose that the differences in morphology are due largely to environmental effects on growth during juvenile stages. The electrophoretic data indicate that Newfoundland and western Gulf of St. Lawrence snow crabs differ genetically from each other and from the Cape Breton Island snow crabs; therefore, they represent two different "genetic" stocks. Eastern and western Cape Breton Island snow crabs did not exhibit electrophoretic differences and, thus, they represent a single genetic stock. Genetic exchange between Atlantic Canadian snow crab populations appears possible through larval dispersal. There is a widely different degree of resilience to exploitation and response to the same management strategy between eastern and western Cape Breton Island snow crab populations; hence, a phenotypically and/or genotypically defined stock is not necessarily a useful management tool. Stocks may be subdivided into more meaningful management units that reflect intra-stock factors such as growth and recruitment patterns.

On compare les caractères morphométriques, méristiques et électrophorétiques et les données sur la fertilité du crabe des neiges, *Chionoecetes opilio*, adulte peuplant l'ouest du golfe du Saint-Laurent, les eaux à l'est et à l'ouest de l'île du Cap-Breton et les eaux à l'est de Terre-Neuve. Les caractères morphométriques et méristiques et les données sur la fécondité révèlent que les crabes des neiges présents dans ces quatre régions sont morphologiquement et biologiquement différents ; ils représent donc quatre stocks « phénotypiques » ou « biologiques ». On formule l'hypothèse que les variations morphologiques sont principalement causées par l'incidence environnementale sur la croissance au cours des stades juvéniles. Les données électrophorétiques révèlent que le crabe des neiges des eaux de Terre-Neuve et celui de l'ouest du golfe du Saint-Laurent sont génétiquement différents, en plus d'être différents de celui des eaux de l'île du Cap-Breton ; on est donc en présence de deux différents stocks « génétiques ». Les individus capturés à l'est et à l'ouest de l'île du Cap-Breton n'ont pas montré de variations électrophorétiques ; ils constituent donc un seul stock génétique. Un échange génétique entre les populations de crabe des neiges peuplant les eaux canadiennes de l'Atlantique semble possible par la dispersion de larves. Il existe un degré très variable d'adaptation à l'exploitation et de réaction à la même stratégie de gestion entre les populations présentes à l'est et à l'ouest de l'île du Cap-Breton. En conséquence, un stock phénotypiquement défini n'est pas nécessairement un outil de gestion utile. Les stocks peuvent être subdivisés en unités de gestion plus représentatives qui traduisent des facteurs propres au stock comme les régimes de croissance et de recrutement.

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The snow crab, *Chionoecetes opilio* (O. Fabricius), is a large spider crab (Majidae, Oregoniinae) that inhabits deep, cold waters in the Northwest Atlantic and North Pacific oceans and the Sea of Japan. In Atlantic Canada, commercial concentrations of snow crab occur in the Gulf of St. Lawrence, around Cape Breton Island, and off the coasts of Labrador and Newfoundland (Elner 1982a).

Adult snow crabs in the Northwest Atlantic are most abundant at depths of 60–200 m on mud or mud–sand–gravel bottoms where temperatures remain between −1°C and 4°C (Brunel 1960; Squires 1966; Powles 1968; Watson 1969). Female snow crabs undergo a terminal molt to maturity and reach a maximum size of 47–95 mm carapace width (CW) (Ito 1963; Watson 1970a; Elner and Robichaud 1983a). Males continue to molt

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TABLE 1. Sample sites and collection details for adult male and female snow crabs collected for morphometric, meristic, and fecundity analyses.

Sample site	No. collected		Location		Depth (m)	Date
	Males	Females	Lat.	Long.		
Newfoundland (Port-de-Grave)	50	51	47°46′	52°46′	68–189	Aug. 23, 1980
Eastern Cape Breton Island (Gabarus)	101	98	45°45′	59°56′	109–155	Aug. 25, 1980
Western Cape Breton Island (Pleasant Bay – Cheticamp)	34	85	46°55′	61°00′	50–159	July 8, 1980
	77	34	46°53′	59°58′	124–135	July 23, 1980
Western Gulf of St. Lawrence (Anticosti)	174	99	50°07′	64°44′	65–207	Aug. 25–30, 1980

after attaining maturity at 51–80 mm CW and can reach a size of approximately 160 mm CW (Watson 1969, 1970a).

Since its inception in 1960, the snow crab fishery has increased steadily in importance to its present status as the most valuable crab species fished in Canadian waters (Elner 1982a) and the fourth most valuable fishery in Atlantic Canada. Female snow crabs are not commercially fished and the reproductive potential of the resource appears unaffected by the commercial harvesting of mature males ≥95 mm CW (Elner and Robichaud 1983a). However, as the unpredictable trends in the Atlantic snow crab fishery demonstrate, the relationships between stock and recruitment are not clear (Bailey 1982; Elner 1982a, 1982b; Waiwood and Elner 1982). The wide variation in the response and resilience of various snow crab populations to fishing pressure and management strategies (Elner 1982a, 1982b) leads to the hypothesis that Gulf of St. Lawrence, Cape Breton Island, and Newfoundland snow crab populations[3] represent different stocks[4] whose integrity depends on the amount of interaction (probably in the form of larval exchange) with other stocks. Mark–recapture studies off Cape Breton Island and Newfoundland have not revealed either extensive or clear patterns of movement by male snow crabs (Elner 1982a; D. M. Taylor, Department of Fisheries and Oceans, St. John's, Nfld., unpubl. data). In the Gulf of St. Lawrence, the majority of marked snow crabs have been recaptured within 15 km of the release point (Watson 1970b; Watson and Wells 1972).

The delineation of stocks has remained an important concern in fisheries management (Ihssen et al. 1981a). Although various approaches have been applied to the problem of stock delineation, the use of multivariate statistical comparisons of morphological characteristics and electrophoresis has gained acceptance among fisheries scientists (Saila and Flowers 1969; Messieh and Tibbo 1971; Parsons and Hodder 1971; Johnson et al. 1972, 1973, 1974; Messieh 1975; Smith et al. 1980; Lindsey 1981; Mulley and Latter 1981a, 1981b). Using such techniques, differences in morphometric, meristic, and/or electrophoretic characteristics are used to infer phenotypic and/or genotypic differences between individuals. To date, these types of studies on decapod crustaceans in the Northwest Atlantic have been restricted to the American lobster, *Homarus americanus* (Milne-Edwards), and have met with limited success (Barlow 1969; Saila and Flowers 1969; Barlow and Ridgway 1971; Tracey et al. 1975; Campbell and Mohn 1982).

In this paper, we document the morphometric, meristic, fecundity, and electrophoretic characteristics of four Northwest Atlantic snow crab populations. In addition, we reared snow crab larvae in the laboratory to elucidate the possibility for current-mediated larval exchange between Atlantic snow crab populations. Given the existence of phenotypic and genotypic differences between the populations, we investigated whether they provide a viable means of delineating snow crab stocks for management purposes.

Materials and Methods

A total of 813 mature male and female snow crabs were collected for morphometric and meristic analyses from sample areas off St. John's, Nfld.; eastern Cape Breton Island (off Gabarus); western Cape Breton Island (off Pleasant Bay and Cheticamp); and in the western Gulf of St. Lawrence (off northwestern Anticosti Island) (Table 1; Fig. 1). Crabs were captured with commercial crab traps (1.5 × 1.5 × 0.6 m steel frames covered by 90-mm mesh). The crabs were then killed by exposure at air temperature, preserved in 10% formalin–seawater, and transported to the Department of Fisheries and Oceans, Biological Station, St. Andrews, N.B. (SABS), for dissection and measurement. The sex, 40 morphometric, and 8 meristic (discrete or discontinuous) characters were recorded for each crab (Fig. 2, 3, 4). Carapace and appendage measurements (Fig. 2, 3) were taken to the nearest 0.1 mm, using dial read-out calipers. Gill measurements were made by using a dissecting microscope and precalibrated ocular micrometers, to the nearest 0.1 mm. All appendages and gills counted were from the right side of the body.

Two partitioning regimes were applied to the data. The first regime consisted simply of separating the data according to sex before analysis. In the second regime, crabs of each sex were arranged into small (males ≤80 mm CW; females ≤60 mm CW), medium (males 80.1–100.0 mm CW; females 60.1–70.0 mm CW), and large (males >100.0 mm CW; females >70.1 mm CW) and each size group was analysed. The analysis utilized was the SPSS version of discriminant function analysis (Klecka 1975), using no a priori probabilities of membership or weighting procedures, and seeking to maximize the minimum Mahalanobis distance between the two closest groups.

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[3] "Population" refers to any spatially, temporally, or artificially (i.e. by management unit) delineated intraspecific group of organisms.

[4] For the purpose of this paper, "stock" will refer to an intraspecific group of individuals exhibiting unique phenotypic, genotypic, or biological attributes.

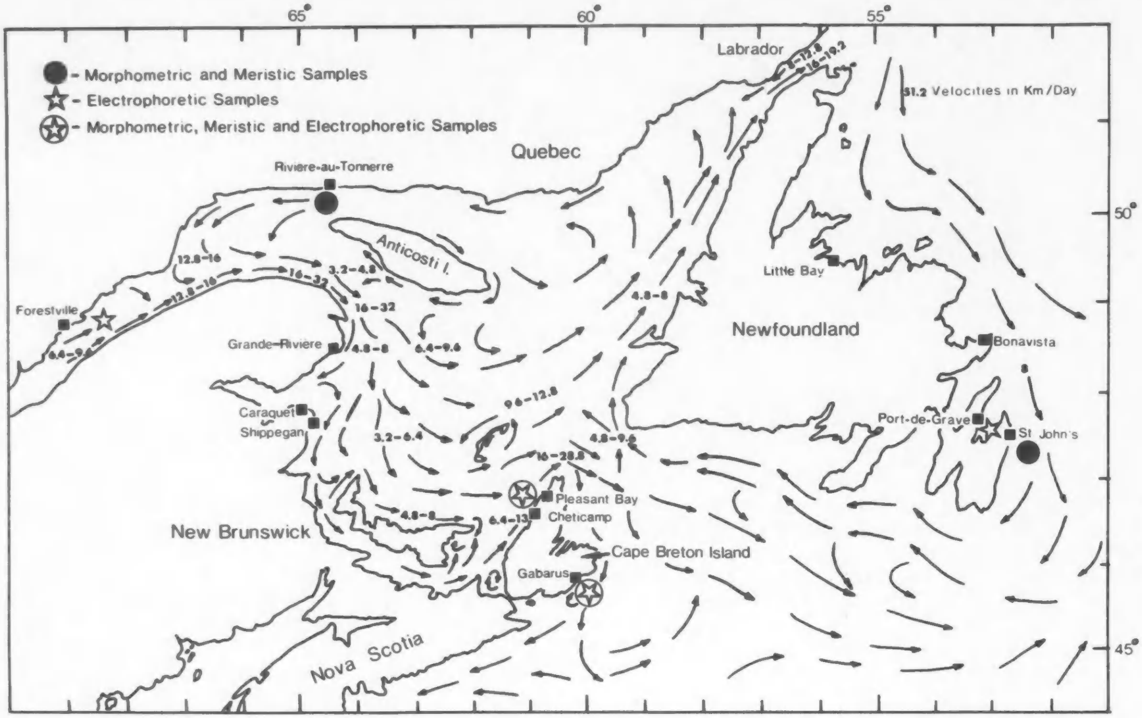
65°
60°
55°
50°
45°
● - Morphometric and Meristic Samples
☆ - Electrophoretic Samples
- Morphometric, Meristic and Electrophoretic Samples
51.2 Velocities in Km/Day
Labrador
8–12.8
16–19.2
Quebec
Riviere-au-Tonnerre
Anticosti I.
12.8–16
3.2–4.8
16–32
12.8–16
16–32
Forestville
6.4–9.6
Grande-Riviere
4.8–8
6.4–9.6
4.8–8
Little Bay
Newfoundland
Bonavista
Caraquet
Shippegan
9.6–12.8
3.2–6.4
4.8–9.6
16–28.8
Port-de-Grave
St John's
Pleasant Bay
Cheticamp
4.8–8
6.4–13
New Brunswick
Cape Breton Island
Gabarus
Nova Scotia

FIG. 1. Typical Atlantic summer surface circulation patterns (after Hachey 1961; Bumpus and Lauzier 1965; Trites 1970; Kudlo and Burmakin 1972; Sutcliffe et al. 1976) in relation to snow crab sample sites.

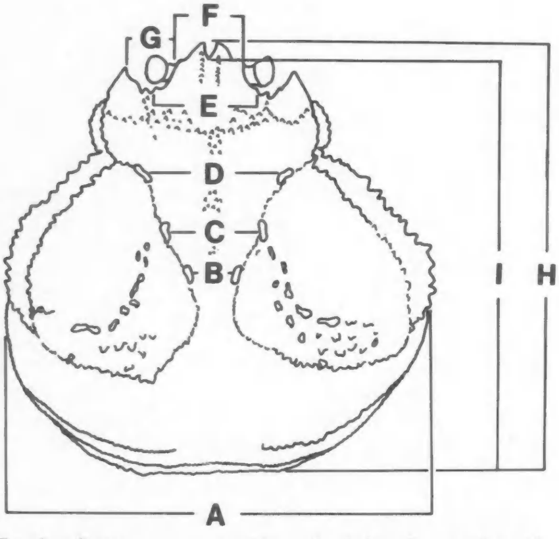

FIG. 2. Carapace measurements made during the morphometric analyses of four Atlantic snow crab populations. A, carapace width; B, distance between third dorsal tubercles; C, distance between second dorsal tubercles; D, distance between first dorsal tubercles; E, rostrum width at base; F, rostrum width at tip; G, orbit width; H, carapace length; I, notch length.

Estimates of fecundity were made for all females from each sample area. The egg-mass from each female was carefully removed from the pleopods and dried to constant weight at approximately 70°C. The dry weight of each egg-mass (total weight of the egg-mass, TWEM) was recorded to the nearest milligram. From each area, a subsample of 10 females was taken. From each of these females, four samples of 30 dried eggs were weighed to the nearest microgram, using a Cahn electrobalance. The mean weight of an egg (WE) was then calculated as follows:

$$(1) \quad \text{Mean weight per egg (WE)} = \Sigma \frac{\text{Weights 1–4}}{120}$$

where weights 1–4 are the weights of each 30-egg sample.

Mean weight per egg (WE) was regressed against carapace width, using a geometric mean regression as outlined by Haynes et al. (1976), and was compared between areas, using a one-way analysis of variance.

Fecundity estimates were made as follows:

$$(2) \quad \text{Fecundity of female}_{AN} = \frac{\text{TWEM}_{AN}}{\text{WE}_{A}}$$

where A = area and N = sample number of the female.

An analysis of covariance was used to compare TWEM, as it covaries with carapace width, between areas.

Samples for electrophoretic analysis, consisting of the right

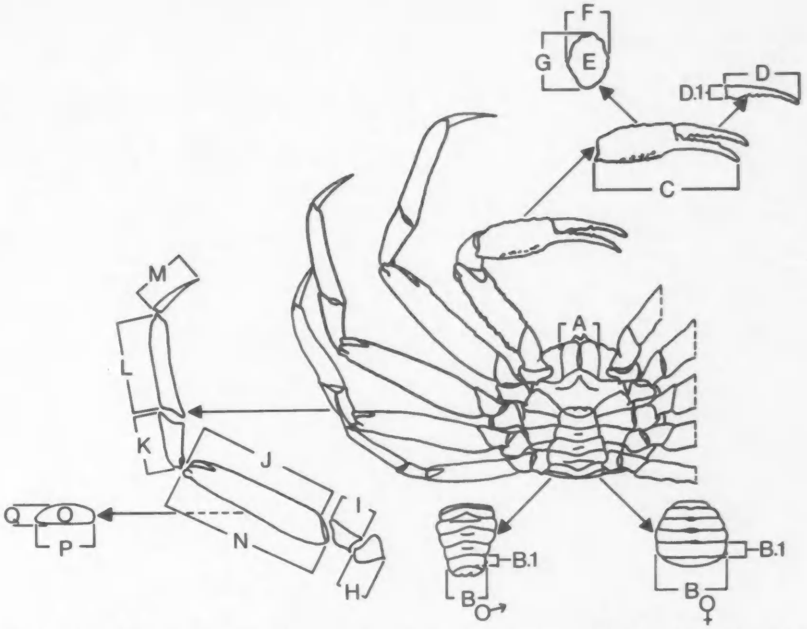

FIG. 3. Appendage, abdomen, and ventral carapace measurements made during the morphometric analysis of four Atlantic snow crab populations. A, pterygostomium width; B, width of the fifth abdominal segment; B.1, length of the fifth abdominal segment; C, length of the first propodus; D, length of the first dactylus; D.1, width of the first dactylus; E, cross-section of the first propodus at its widest point; F, width of the first propodus; G, depth of the first propodus; H, length of coxa of cheliped and periopods; I, length of basis of cheliped and periopods; J, inside length of merus of cheliped and periopods; K, length of carpus of cheliped and periopods; L, length of propodus of periopods; M, length of dactylus of periopods; O, cross-section of merus of cheliped and periopods at the widest point; P, width of merus of cheliped and periopods; Q, thickness of merus of cheliped and periopods.

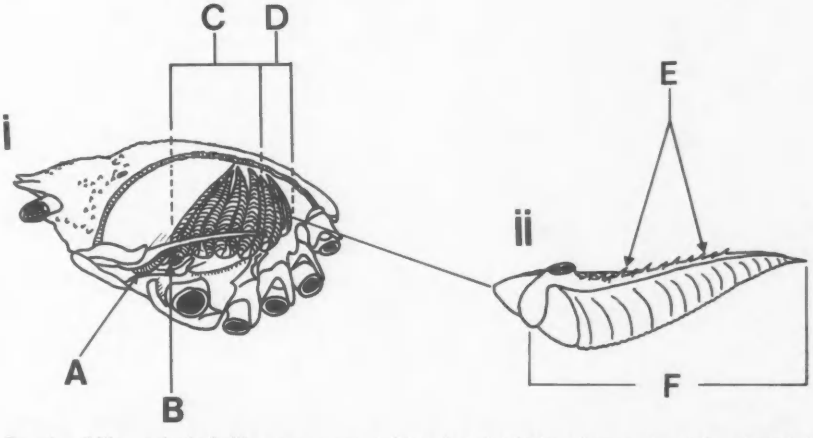

FIG. 4. Gills, method of gill measurement, and location of gill spines for morphometric and meristic analysis of four Atlantic snow crab populations. (i) Thorax of *C. opilio* dissected from the left side to show (A) first podobranch, (B) second podobranch, (C) arthrobranchs, and (D) pleurobranchs. (ii) Isolated pleurobranch of *C. opilio* showing (E) gill spines and (F) gill length dimension.

cheliped of hard-shelled males of legal size (⩾95 mm CW), were collected from the western Gulf of St. Lawrence off Forestville, Que. (August 19, 1982; depth 55–146 m); western Cape Breton Island off Pleasant Bay (July 28, 1982; depth 100–146 m); eastern Cape Breton Island off Gabarus (July 29, 1982; depth 132–183 m); and Newfoundland off Port-de-Grave (November 11, 1982; depth 271 m) (Fig. 1). The samples were stored in dry ice or in freezers at −35°C until transported to the University of Windsor, Windsor, Ont., where a disc polyacrylamide electrophoretic survey (Ornstein 1964) of 10 enzyme

TABLE 2. Enzymes surveyed during electrophoretic examination of cheliped muscles from snow crab collected from sites off Newfoundland, eastern Cape Breton Island, western Cape Breton Island, and the western Gulf of St. Lawrence.

Enzyme	Abbreviation	Type of gel used	
		Starch	Polyacrylamide
α-Esterase	EST (EC 3.1.1.2)	×	×
Glucose-6-phosphate dehydrogenase	G-6-PDH (EC 1.1.1.49)	—	×
Glutamate oxaloacetic transaminase	GOT (EC 2.6.1.1)	×	×
Phosphoglucose isomerase	PGI (EC 5.3.1.9)	—	×
Lactate dehydrogenase	LDH (EC 1.1.1.27)	×	×
Leucine amino peptidase	LAP (EC 3.4.11.1)	—	×
Phosphoglucomutase	PGM (EC 2.7.5.1)	—	×
Fumarase	FUM (EC 4.2.1.2)	×	×
Xanthine dehydrogenase	XDH (EC 1.2.1.37)	—	×
Malate dehydrogenase	MDH (EC 1.1.1.37)	×	×
General protein	GP	×	—
Aconitase	Acon (EC 4.2.1.3)	×	—
Malic enzyme	ME (EC 1.1.1.40)	×	—
Isocitrate dehydrogenase	IDH (EC 1.1.1.42)	×	—

TABLE 3. Frequency of esterase phenotypes for four Atlantic populations of snow crabs (S_1–S_3 = slow bands; M = medium band; F = fast band).

Phenotypes	Sample population			
	Newfoundland	Eastern Cape Breton Island	Western Cape Breton Island	Western Gulf of St. Lawrence
MF	30 (48.4%)	0 (—)	0 (—)	11 (20.0%)
S_3 MF	5 (8.1%)	60 (96.8%)	54 (93.1%)	33 (60.0%)
S_2 S_3 MF	4 (6.4%)	1 (1.6%)	3 (5.2%)	5 (9.5%)
S_1 S_2 S_3 MF	11 (17.7%)	0 (—)	0 (—)	3 (5.4%)
S_1 S_2 MF	6 (9.8%)	0 (—)	0 (—)	1 (1.8%)
S_1 MF	1 (1.6%)	0 (—)	0 (—)	0 (—)
S_2 MF	4 (6.4%)	0 (—)	0 (—)	2 (3.7%)
S_1 S_3 MF	1 (1.6%)	1 (1.6%)	1 (1.7%)	0 (—)
Total	62	62	58	55

systems (Table 2) was made for merus and propodus muscles from 10 sample chelipeds from each of the four sample areas. Esterases were surveyed for all sample chelipeds (55–62 per area, Table 3).

To obtain larvae for laboratory rearing, five ovigerous *C. opilio* females were collected off Cheticamp, Cape Breton Island (46°43′N, 61°12′W), on November 25, 1980. The females were transported to SABS where they were held individually in 68- to 91-L aquaria at 3–5°C until the hatching of their larvae had been completed. Upon hatching, larvae were transferred to individual rearing containers in a flow-through rearing system modelled after that utilized by D. E. Aiken for American lobster culture at SABS. Water temperature in the rearing system was maintained at a mean temperature of 11°C (range: 10.0–12.5°C) and salinity of 27.9–31.9‰ throughout the rearing period. The larvae were fed daily with freshly hatched brine shrimp, *Artemia salina* (Linnaeus), nauplii. The numbers of larvae molting or dying were recorded daily. Dead larvae and exuviae were removed daily along with excess *A. salina* from the previous feeding.

Results

Morphometrics and Meristics

With all 48 morphometric and meristic characters, the proportion of both males and females of all sizes (the first partitioning regime) properly classified by discriminant function analysis (i.e. their predicted group membership coincides with their actual group membership) exceeds 83% for all areas (Table 4). A higher percentage of females than males was properly classified for areas other than western Cape Breton Island (Table 4). Newfoundland exceeded the other areas in the percentage of both males and females properly classified (Table 4).

The mean percentage of males and females properly classified according to area in small, medium, and large size groups (the second partitioning regime) was 87.9, 79.4, and 75.2, respectively, for males and 93.3, 69.1, and 68.1, respectively, for females.

A comparison of the percentage of individuals properly classified versus the number of variables used for classification in the discriminant function analysis (Fig. 5) indicates that the

TABLE 4. Results of a discriminant function classification (based on 48 morphometric and meristic characters) of four Atlantic snow crab populations. Females from all areas correctly classified = 89.9%; males from all areas correctly classified = 85.4%.

			Predicted group membership (%)							
	No. of cases		Newfoundland		Eastern Cape Breton Island		Western Cape Breton Island		Western Gulf of St. Lawrence	
Actual group	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females
Newfoundland	50	51	90.0	94.1	2.0	0.0	0.0	2.0	8.0	3.9
Eastern Cape Breton Island	101	98	0.0	2.0	83.2	90.8	5.9	4.1	10.9	3.1
Western Cape Breton Island	121	119	3.3	4.2	7.4	4.2	87.6	86.6	1.7	5.0
Western Gulf of St. Lawrence	174	99	4.0	3.0	11.5	3.0	0.6	3.0	83.9	90.9

TABLE 5. Estimates of total fecundity and regressions of fecundity (Y) with carapace width (X in mm) for female snow crabs from four Atlantic snow crab populations (R = correlation coefficient).

	No. of females sampled	Fecundity regression	R	Mean fecundity	Fecundity range
Newfoundland	51	$Y = 6.4080X^{2.1690}$	0.777	52 000	37 900 – 81 200
Eastern Cape Breton Island	115	$Y = 14.8371X^{1.9859}$	0.660	80 100	42 300 – 120 400
Western Cape Breton Island	98	$Y = 38.4554X^{1.7649}$	0.635	74 500	32 600 – 128 400
Western Gulf of St. Lawrence	98	$Y = 13.2530X^{1.9922}$	0.747	58 800	12 100 – 122 900

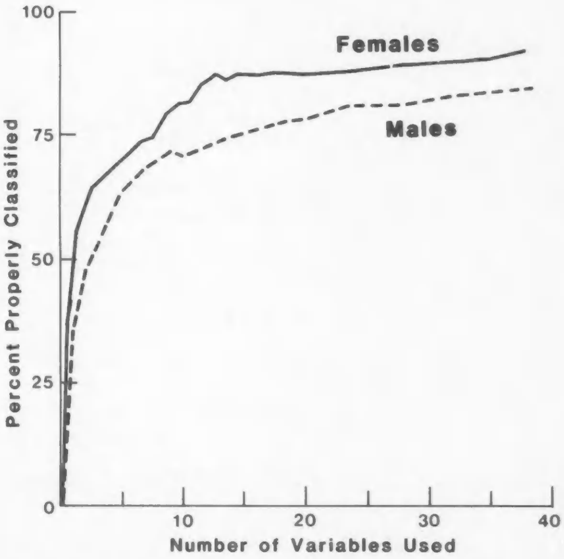

FIG. 5. Percentage of male and female snow crabs properly classified during discriminant function analysis versus the number of variables used during the analysis.

use of 12–15 discriminating variables would provide at least 70% proper classification and be logistically more effective than the 48 variables we used.

Fecundity

The mean weight per egg (WE) did not correlate with female size (CW) for any of the areas. In addition, analysis of variance results indicated a greater variance in WE within areas than between them. For this reason, WE for all females were pooled to give an overall mean of 5.81×10^{-15} g per egg (WE_A in Equation 2), which was used in calculating fecundity. Fecundity estimates ranged from 12 100 to 128 400 eggs per female (Table 5). The total weight of the egg mass (TWEM), as it covaries with carapace width, was found to vary significantly ($p < 0.0001$) between areas with Duncan's multiple range test grouping each area separately ($p < 0.05$). The areas were grouped from highest to lowest TWEM as follows: eastern Cape Breton Island, western Cape Breton Island, western Gulf of St. Lawrence, Newfoundland.

Electrophoresis

Of those enzymes that resolved well (LDH, MDH, fumerase, G-6-PDH, and esterases) only esterases exhibited polymorphisms. Eight phenotypes (banding patterns) were observed (Table 3). Only the Newfoundland snow crabs exhibited all eight esterase phenotypes (Table 3). Six phenotypes were present in the western Gulf of St. Lawrence snow crabs and only three phenotypes were present in the eastern and western Cape Breton Island snow crabs (Table 3). A chi-square comparison of phenotype frequencies between areas (Table 6) shows that eastern and western Cape Breton Island snow crabs do not differ

TABLE 6. Comparison of esterase phenotypes for four Atlantic snow crab populations. H_0: phenotype frequencies do not differ significantly between areas; *significantly different, $p < 0.05$ (calculated χ^2 values).

	Western Gulf of St. Lawrence	Western Cape Breton Island	Eastern Cape Breton Island
Newfoundland	(40.8)*	(92.8)*	(100.3)*
Western Gulf of St. Lawrence	—	(23.5)*	(28.2)*
Western Cape Breton Island	—	—	(1.2)

significantly from each other, while both the Newfoundland and western Gulf of St. Lawrence snow crabs differ significantly from each of the other areas.

Larval Rearing

Snow crab larvae hatched from March 25 to late April and exhibited high mortality rates in the flow-through rearing system we used. Only three larvae reached the megalopa stage and only one attained the first crab stage. The mean length of time (days after hatching) required to attain the second zoea, megalopa, and first crab stages was 25.7 d (*n* = 15, range: 16–29), 36.7 d (*n* = 3, range: 35–38), and 71 d (*n* = 1), respectively.

Discussion

Morphometrics and Meristics

Invertebrates, such as crustaceans, generally exhibit little morphological change in response to short-term changes in their environments. In addition, their rigid exoskeleton often allows for more precise morphometric measurements compared with "softer bodied" vertebrates. Such characteristics suggest that morphological comparisons of crustacean populations may provide useful evidence for delineating stocks. This contention is supported by the results of the present study (Table 4), which meet or exceed those of previous similar studies (Saila and Flowers 1969; Messieh 1975; Foottit and Mackauer 1980; Ihssen et al. 1981b; Almeida 1982; Campbell and Mohn 1982) and indicate a high degree of phenotypic distinctness between the four snow crab populations sampled.

If a "stock" is considered to be an intraspecific group of individuals that exhibit specific phenotypic attributes in response to environmental and/or genetic factors, then from our results of the morphometric, meristic, and fecundity comparisons we propose that the four snow crab populations sampled represent four distinct stocks. As discussed by Booke (1981), it is often difficult to distinguish between genetic and environmental effects on phenotypic characteristics. The physical characteristics of the adult snow crab environment in all four sample areas are similar and temporally homogeneous; therefore, one might assume that the majority of the phenotypic variability observed between areas would be due to genetic dissimilarities. However, such an assumption fails to consider the effect of the environment on early life history stages.

We hypothesize that the phenotypic differences observed between snow crab populations are due to morphological differentiation in response to environmental factors during the juvenile stages when the crabs are in relatively heterogeneous environments (Miller 1975; Adams 1979; Desrosiers et al. 1982; D. A. Robichaud, Biological Station, St. Andrews, N.B., unpubl. data). As the crabs grow larger and move to their relatively homogeneous adult environments, they tend to converge in their morphological attributes. This convergence would be cut short in females due to the terminal molt at maturity, but should extend on through the life of the adult males. The hypothesis is supported by our results which indicate that females and small crabs are phenotypically more distinct between areas than large male crabs.

Fecundity

The results of the fecundity against CW comparisons indicate that the four populations studied are distinct. Thus, the fecundity data support the morphometric and meristic results in suggesting that the four populations represent separate stocks.

Electrophoresis and Larval Duration

Previous authors (Horrall 1981; Booke 1981; Kutkuhn 1981) have implied that for the formation and maintenance of stocks "a moderately high degree of reproductive isolation is necessary" (Horrall 1981). Such a view implies a need for genetic isolation, and that stocks should be defined as intraspecific groups of individuals exhibiting similar genetic attributes.

From electrophoretic studies it was inferred that decapod crustaceans, especially large, mobile species, exhibit low levels of genetic variability (Nelson and Hedgecock 1980). Esterases are often found to exhibit the greatest amount of polymorphism and have been genetically interpreted for some decapods (Smith et al. 1980; Turner and Lyerla 1980). However, esterases are often weak and unstable and there is evidence that their isozymes may change due to nongenetic causes, such as ontogenetic or physiological state (McWhinnie and Corkill 1964; Manwell and Baker 1970; Johnson et al. 1974; Kannupandi 1980).

The differences in esterase patterns we observed were not amenable to genetic interpretation (such as deviations from Hardy–Weinberg equilibria) due to our inability to describe their genetic basis; therefore, for this reason and those mentioned previously, they were interpreted as phenotypic expressions of probable genotypic differences. Our results indicate that the snow crabs from Newfoundland and the western Gulf of St. Lawrence possibly differ genetically from each other and from those of eastern and western Cape Breton Island, and represent separate genetic stocks. The results also indicate that eastern and western Cape Breton Island snow crabs represent a single genetic stock.

If genetic characteristics of populations (as opposed to phenotypic and/or biological characteristics) are accepted as the basis for delineating stocks, then a reason for these characteristics should be postulated. All of the snow crab areas sampled are geographically separated (Fig. 1). This fact, coupled with the observation from tagging studies that adult snow crab movements are limited, implies a lack of interbreeding between adults from different areas, and provides an explanation for the genotypic differences we inferred. Why then do the eastern Cape Breton Island and western Cape Breton Island populations appear genetically similar? The answer may lie in the exchange of pelagic larvae.

Kon (1970) derived estimates of larval duration in relation to water temperature. His estimate for total duration at 11°C of 69–73 d corresponds well to the 71-d estimate we obtained. The median surface water temperature in the Gulf of St. Lawrence, Cape Breton Island, and southern Newfoundland regions for the period of May through August (the period when *C. opilio* larvae are most likely to be present in surface waters) is 11°C (Lauzier and Hull 1969). Assuming a pelagic larval duration of 71 d for the areas studied, and given surface current velocities of 3.2–32.0 km/d (2–20 mi/d; Trites 1970; Fig. 1), distances of 227–2272 km can be estimated for the passive transport of snow crab larvae in surface currents. These estimates assume straight-line movements and may not be entirely realistic; however, they do serve to illustrate the potential for transport and exchange of snow crab larvae. When the estimates of larval transport by surface currents are considered in conjunction with typical summer surface circulation patterns (Fig. 1), it is possible for genetic exchange through larval recruitment to occur between all Atlantic snow crab grounds. The magnitude of larval exchange between areas would be affected by oceanographic patterns and should be directly proportional to the distance between areas, the velocity of surface currents, and larval duration. Eastern and western Cape Breton Island snow crab grounds are close geographically with strong currents running between them (Fig. 1); thus, larval recruitment to the eastern Cape Breton Island snow crab grounds possibly originates from snow crab populations off western Cape Breton Island. Such a scenario would account for the apparent genetic similarity of the eastern (Gabarus) and western (Pleasant Bay) Cape Breton Island snow crab stocks as inferred by our electrophoresis results.

The Commercial Fishery

The results of the morphometric, meristic, fecundity, and electrophoretic studies indicate that Newfoundland and western Gulf of St. Lawrence snow crab populations represent separate phenotypic and genotypic stocks differing significantly from each other and from Cape Breton Island snow crab populations. With respect to the eastern and western Cape Breton Island snow crab populations, the electrophoretic results conflict with those of the morphometric, meristic, and fecundity studies by indicating that they form a single "genetic" stock.

Given that stock definition is frequently attempted to define management units, we can review the applicability of the "single-stock-management-unit" concept, by comparing the history of the two areas within the Cape Breton Island "genetic" snow crab stock. Since 1978, the management strategy for eastern and western Cape Breton Island snow crab grounds has been to develop a stable, supplementary fishery with a large number of participants (Elner 1982b). Consequently, total allowable catch restrictions in these areas were based on a strategy of permitting only the harvest of biomass equivalent to the calculated growth and recruitment additions for the previous year, in an attempt to maintain a large, stable stock (Elner 1982b). Both areas were expected to respond similarly to this management strategy. However, within four fishing seasons, catch rates and the commercial biomass in eastern Cape Breton Island collapsed (Elner 1982b; Elner and Robichaud 1983b). In contrast, catch rates and commercial biomass have remained relatively stable in western Cape Breton Island (Elner 1982b). The substantial differences in historical landings between these two snow crab grounds appear more remarkable given that the areas are of approximately equal size (2750 km^2 vs. 2059 km^2), have similar numbers of fishermen (27 vs. 26), and are separated by less than 160 km of landmass. Furthermore, the number of snow crab females in the Atlantic can be assumed to approximate prefishery levels and, hence, decreases in egg production are unlikely to be a factor in the collapse.

Evidence accrued from stock assessments (Elner and Robichaud 1983b) indicates that eastern Cape Breton Island snow crab grounds are unproductive in terms of growth and recruitment. Possibly, the eastern areas, being at the southern edge of known commercial snow crab concentrations in the Atlantic, represent marginal grounds in terms of habitat. Thus, although comparisons of biomass, catch rates, and size frequencies for eastern Cape Breton Island reveal apparent recruitment failures, it may be that the situation represents the normal pattern of production.

Probably there is little endemic recruitment within the eastern Cape Breton Island snow crab population. Larvae released from this population may become entrained in local gyres or swept northeast toward Newfoundland (Fig. 1), but the predominant surface currents in the area would tend to disperse pelagic larvae south, down the coast of Nova Scotia or out into the Atlantic (Fig. 1). *Chionoecetes opilio* larvae are present throughout the Scotian Shelf, with early larval stages more abundant in the north, and the megalopa stage found only in the south (Roff et al. 1984). This type of larval distribution, plus the presence of small numbers of snow crab off Grand Manan Island in the Bay of Fundy, and in the Gulf of Maine (M. J. Dadswell, Biological Station, St. Andrews, N.B. pers. comm.), supports the possibility of a large, southward loss of *C. opilio* larvae from eastern Cape Breton Island. Thus, the eastern Cape Breton Island snow crab population was probably built up over time through trickles of larval recruitment largely from western Cape Breton Island. Such a scenario would account for the initially high catch rates and landings on the grounds, the lack of resilience of the stocks to exploitation, and the subsequent devastation of biomass and catch rates after only a few fishing seasons.

In contrast with the east coast, the management by "stable-stock" policy appears to have succeeded in western Cape Breton Island. Overall annual biomass additions, although variable in periodicity, have appeared relatively large and consistent since 1978 (Elner 1982b). This consistency, despite exploitation rates of 47–64%, has conferred resilience to the western Cape Breton Island stock and has facilitated management.

The experiences of the Cape Breton Island snow crab fishery indicate that the "stock" per se, as defined by genetic and/or phenotypic characteristics, is not necessarily a meaningful management unit. Stocks may be more usefully subdivided into management units that reflect intra-stock factors such as growth and recruitment patterns. Thus, unique phenotypic and/or genotypic characteristics of intraspecific groups of individuals may be useful in the delineation of stocks, but should not be accepted as a basis for management strategies until the biotic and abiotic factors governing these characteristics are elucidated.

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Diet and Digestion Rates of Slimy Sculpin, *Cottus cognatus*, in an Alaskan Arctic Lake

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Hershey, A. E., and M. E. McDonald. 1985. Diet and digestion rates of slimy sculpin, *Cottus cognatus*, in an Alaskan arctic lake. Can. J. Fish. Aquat. Sci. 42: 483–487.

In arctic Toolik Lake, slimy sculpin (*Cottus cognatus*) rely on a diet of larval chironomids (Diptera: Chironomidae). Dry weight of sculpin gut contents was not correlated with fish wet weight. This finding, combined with age and growth data, suggested that sculpin may be food limited in Toolik Lake, particularly as they approach reproductive size. Since three taxonomically distinct chironomids were digested at similar rates, one chironomid species was used as a marker to measure gut passage. Gut passage rate as a function of temperature fits an inverse quadratic model slightly better than a negative exponential model. Sculpins took approximately 1 d to digest food at typical summer temperatures (8–16°C), but approximately 2 d at a typical winter temperature (4°C). Since winter is three times longer than summer, winter feeding by sculpins may have greater impact on chironomid density than summer feeding. If sculpin are important in the diet of other Toolik Lake fishes, they may serve as an important trophic link between benthic and pelagic production.

Dans le lac Toolik (Arctique), le chabot visqueux (*Cottus cognatus*) se nourrit de larves de chironomidés. Le poids sec des contenus stomaceux n'était pas en corrélation avec le poids humide du poisson. Ce fait, combiné avec les données sur l'âge et la croissance, porte à croire que le chabot est confiné au lac Toolik à cause de ses besoins alimentaires surtout quand il approche de la maturation sexuelle. Comme trois espèces distinctes de chironomidés étaient digérées à des taux semblables, une seule a été utilisée comme marqueur pour quantifier le temps d'évacuation. Ce taux en fonction de la température épouse mieux une courbe quadratique inverse qu'une courbe exponentielle négative. À des températures estivales normales (8–16°C), il fallait environ 1 d au chabot pour digérer la nourriture et environ 2 d à des températures hivernales normales (4°C). Comme l'hiver est trois fois plus long que l'été, l'alimentation du chabot en hiver peut avoir une plus grande incidence sur la densité des chironomidés que celle de l'été. Si le chabot est une grande composante du régime d'autres poissons peuplant le lac Toolik, il sert peut-être d'important lien trophique entre la production benthique et la production pélagique.

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Slimy sculpins, *Cottus cognatus*, are common, widely distributed fish that inhabit cold, well-oxygenated waters (Van Vliet 1964; Scott and Crossman 1973; Petrosky and Waters 1975; Craig and Wells 1976). They often occur with various salmonids (Salmonidae and Coregonidae) and burbot (*Lota lota*), and may be important in the diet of those fishes (Moyle 1977). Individual growth rate of slimy sculpins appears to be determined by temperature and food availability. Van Vliet (1964) found that a stream population that had a more reliable year-round food supply grew faster and reproduced more quickly than a nearby lake population. The lake population studied by McDonald et al. (1982) grew more slowly than the stream population studied by Petrosky and Waters (1975), although both were at the same latitude (68°N). This difference may have been due either to greater food supply in the stream or to climatic differences between the sites (McDonald et al. 1982).

Slimy sculpins feed on benthic invertebrates. Chironomids (Diptera: Chironomidae) are a major item in the diet of slimy sculpins (Craig and Wells 1976), prickly sculpins (*Cottus asper*) (Broadway and Moyle 1978), and mottled sculpins (*Cottus bairdii*) (Zarbock 1952; Bailey 1952). Bailey (1952) found that mottled sculpins relied mostly on chironomids when small, but as they increased in size, chironomids became less important in the diet. Diet shifts by sculpins from chironomids to larger insect taxa can be attributed to an increase in mouth size, which permits them to handle larger prey (Northcote 1954).

Gut analyses of fish do not necessarily provide information either on the proportions of prey types eaten or on the amount of food eaten. Prey types may be digested at different rates, particularly if they differ greatly in fat content (Elliot 1972). The assumption that digestion rate for all prey types is the same can be misleading when estimating the proportions of different prey types in a predator's diet (Peterson and Bradley 1978). The rate of passage through the gut of any prey type appears to depend on temperature in all fish studied (Van Vliet 1964; Elliot 1972; Persson 1981; Ryer and Boehlert 1983). An exponential decay model is usually used to describe the relationship between digestion and temperature (Elliot 1972; Ryer and Boehlert 1983), but other models might also be appropriate.

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Here, we examine diet and digestion of the slimy sculpin in Toolik Lake in arctic Alaska (68°37′N, 149°35′W). Although the sculpin population of Toolik has been well studied (Cuker 1981; McDonald et al. 1982; Hershey 1983, 1985b), further study is warranted because sculpins may be unusually important in the trophic structure of the lake. The benthic community in Toolik Lake is dominated by chironomids and snails (Hershey 1983). Insect taxa that are eaten by large sculpin elsewhere are few and scarce in Toolik Lake (Hershey 1983). Hershey (1985b) found that slimy sculpins significantly reduced the density of chironomid larvae in the bare-sediment habitats of Toolik Lake, but had a negligible effect on chironomid density in macrophyte-covered sediments. Whether or not sculpins feed during the winter in Toolik Lake is unknown. However, if they do feed, and even if they digest food much more slowly than at summer temperatures, their impact on the chironomid food resource during the winter could be considerable; winter is three times longer than summer and prey cannot reproduce during the winter.

Study Area

Toolik Lake is a multibasin glacial lake located in rolling tundra on the North Slope of the Alaska Brooks Range along the Trans-Alaska Pipeline Haulroad. The basins are divided by large boulders which form the rocky littoral zone, comprising approximately 25% of the lake area. The remainder of the lake bottom is composed of soft, silty sediments. The lake has a mean depth of approximately 7 m and a maximum depth of 25 m. Approximately 2 m of ice covers the lake from early October to mid-June. During the open water season, Toolik Lake is stratified with the thermocline beginning at 5 m. The epilimnion reaches a maximum summer temperature of 14–16°C.

The fish community of Toolik Lake consists of lake trout (*Salvelinus namaycush*), arctic grayling (*Thymallus arcticus*), round whitefish (*Prosopium cylindraceum*), burbot, and slimy sculpin (O'Brien et al. 1979; McDonald et al. 1982; Hershey 1983). Little is known about the feeding ecology of the salmonids and burbot in Toolik Lake; however, all the fish are known to rely wholly or partly on benthic production. Snails, especially *Lymnaea elodes*, have been frequently found in stomachs of lake trout and round whitefish (O'Brien et al. 1979; Hershey 1983). Small trout and grayling eat zooplankton (Schmidt and O'Brien 1982), but larger grayling eat emerging chironomid pupae and adults (O'Brien et al. 1979; Hershey 1983). The few burbot stomachs that have been examined have contained sculpin (A. E. Hershey, pers. obs.).

Methods

Sculpins were collected from the soft-sediment littoral zone of Toolik Lake during the open water seasons of 1980–82. Unbaited jar traps, fitted with clear plastic funnels (after McDonald et al. 1982), were placed on the sediment surface at depths ranging from 3.5 to 5 m. Nylon lines attached to floats marked the traps so they could be sampled from a boat. In 1980 and 1981, traps were sampled every 2 or 3 d. In 1982, traps were sampled at irregular intervals to collect fish for experiments and gut analyses. However, only fish caught in traps that had been set for 3 h or less were used for gut analyses in 1982.

Sculpins collected in 1981 and 1982 were blotted dry and weighed to the nearest 0.01 g. Only 18 of the 36 sculpins collected in 1980 were weighed. All sculpins were preserved in 10% buffered formalin prior to gut analyses.

Guts were dissected from 51 sculpins. The stomachs and intestines were examined for all prey remains. Prey remains were mounted on glass slides in Amman's lactophenol and identified to lowest possible taxon. Most prey remains were sclerotized head capsules of larval chironomids. Identification to genus was usually possible.

Total dry weight of sculpin gut contents was estimated for sculpins with nonempty guts. This was done by summing the estimated biomass of all chironomid prey items in each sculpin gut. Biomass was calculated from the length – dry weight regressions for Chironomidae given by Smock (1980). Since chironomid prey were usually not intact, the length of a prey item was taken as the median length of that chironomid genus (or species, in some cases) sampled at the study site (Hershey 1985a). Benthic samples were taken on 18 July 1980, 8 July 1981, and 28 July 1981. Since individual size for a chironomid genus varied seasonally (Hershey 1985a), the median lengths used for gut dry weight estimates were those from the sampling date nearest to the catch date of a fish. For example, for fish caught early in July, the lengths from the 8 July 1981 sampling were used.

Many pupae in guts were in poor condition; those that could be identified were all Tanypodinae. All pupae were assigned the dry weight of a 7.0-mm Tanypodinae larva (Smock 1980), which is the approximate size of a Toolik Lake Tanypodinae in the last larval instar (Hershey 1985a).

The calculated dry weight of gut prey was regressed against wet weight of sculpins to determine if gut contents increased with sculpin size. A regression was performed on 1982 fish alone because those fish had been in traps less than 3 h. A separate regression was performed on 1980 and 1981 sculpins with nonempty guts. The slopes of the two regressions were compared using a *t*-test for homogeneity. Since the slopes were homogeneous (see Results), a regression equation was calculated for all sculpins with nonempty guts. If larger sculpins had greater dry weight of gut contents, the regression would yield a positive slope. Thus, the slope of the regression equation was tested to determine if it was significantly different from zero.

To determine digestion rates of different chironomid prey by sculpins, we chose three chironomid prey types: *Stictochironomus rosenschoeldi*, *Heterotrissocladius maeaeri*, and *Procladius* spp. We chose these chironomids because they are common in the soft-sediments of Toolik Lake, are frequently eaten by sculpins, and they represent three different subfamilies of Chironomidae. We assumed that any differences in digestion rates of chironomids by sculpin would be detected by examining the most distantly related chironomid species.

We collected five sculpins from the lake and individually housed them in 28.5 × 17.5 × 12 cm plastic aquaria containing filtered lake water. Sculpin sizes were representative of the sizes in the lake (McDonald et al. 1982), except that no fish under 3 cm were used. Water temperature was not directly controlled, but the aquaria were floated in an insulated water bath to minimize temperature fluctuations. The sculpins were fed a diet of six 10-mm *S. rosenschoeldi*, three 6-mm *H. maeaeri*, and two 6-mm *Procladius* at approximately 17:00 each day. Feces were removed twice daily to discourage reingestion. Water was changed every other day. After 5 d, all fish were sacrificed and preserved in 10% buffered formalin.

We dissected guts from the five sculpins to determine if the prey remaining in guts were proportionate to prey eaten. For each of the three prey taxa, the percentage digested by each sculpin was calculated as follows:

$$\frac{\text{Number fed over 5 d} - \text{number remaining in gut}}{\text{Number fed over 5 d}} \times 100.$$

The percentage digested was compared between the three prey taxa using a one-way ANOVA on the arcsin transformed data.

To determine the rate of gut passage as a function of temperature, we collected sculpins from the lake and housed them in identical plastic aquaria floating in temperature-controlled water baths. One water bath was maintained at 8°C (the approximate lake temperature at the initiation of the experiment) by occasionally adding ice. A second water bath was warmed over a 3-d period to 16°C. A third bath was cooled over a 2-d period by adding jars of ice to the bath. The fish were unfed for 3 d, until all water baths were at the desired temperature. Aquaria were checked twice daily and any feces were removed. The aquaria water was changed every other day with filtered, temperature-equilibrated, lake water.

The fish were fed a diet of four instar IV *Stictochironomus* every 8 h for five feedings. Every 4 h, aquaria were checked for feces, which were removed. On the sixth feeding, all fish were fed five instar IV *Heterotrissocladius*, and then returned to the diet of four instar IV *Stictochironomus* for subsequent feedings. The *Heterotrissocladius* served as a marker. Feces were removed every 4 h and examined for *Heterotrissocladius* head capsules. Gut passage time for each fish was scored as the time required for >50% of the *Heterotrissocladius* meal, or three head capsules, to appear in the feces. Seven sculpins were tested at 4° and 8°C. Eight sculpins were tested at 16°C.

Gut passage rates were fitted to an exponential decay model (Elliot 1972):

$$\ln R = mT + b$$

where R is rate of gut passage (number per hour), T is the temperature (degrees Celsius), and m and b are, respectively, the slope and intercept of the regression equation.

Gut passage rates were also fitted empirically to an inverse quadratic model:

$$R = mT^{-2} + b$$

where the variables and constants are the same as in the exponential decay model.

Results

Gut analyses of 51 sculpins showed that they ate mainly chironomids (Table 1). Larval chironomids, representing 12 genera, comprised 84% of sculpin diet items. *Heterotrissocladius* and *Stictochironomus* were the most frequently eaten larvae, accounting for 56.8% of the prey items. Chironomid pupae comprised 13.6% of the diet items. Only 2.4% of the diet consisted of microcrustaceans, and no other prey types were found (Table 1).

The calculated dry weight of sculpin guts was not related to fish wet weight (Fig. 1). The regression equation for the 26 sculpins that were weighed during 1980 and 1981 was

$$W = 0.042P_W + 1.00 \quad r = 0.287$$

where W = wet weight of fish (grams) and P_W = calculated dry weight of prey (milligrams). A similar regression equation was obtained for the 11 sculpins that were collected from traps tended every 3 h in 1982:

$$W = 0.0045P_W + 1.56 \quad r = 0.028.$$

Neither correlation coefficient was significant ($p > 0.2$). The

TABLE 1. Sculpin gut contents. Entries are mean number of each prey taxon and the percentage of total prey items found in guts of 51 sculpin.

Taxon	$\bar{X}$/gut(SE)	% of total
Orthocladiinae		
Heterotrissocladius	7.5(2.2)	44.4
Parakiefferiella	0.2(0.1)	1.2
Zalutschia	0.1(0.1)	0.6
Psectrocladius	0.3(0.1)	1.8
Cricotopus	0.6(0.2)	3.6
Paracladius	0.2(0.1)	1.2
Tanypodinae		
Procladius	0.5(0.1)	3.0
Ablabesmyia	1.3(0.2)	7.7
Prodiamesinae		
Monodiamesa	0.4(0.2)	2.4
Chironominae		
Stictochironomus	2.1(0.4)	12.4
Tanytarsini	1.0(0.3)	5.9
Crustacea	0.4(0.1)	2.4
Chironomidae pupae	2.3(0.7)	13.6
Total	16.9	100.2

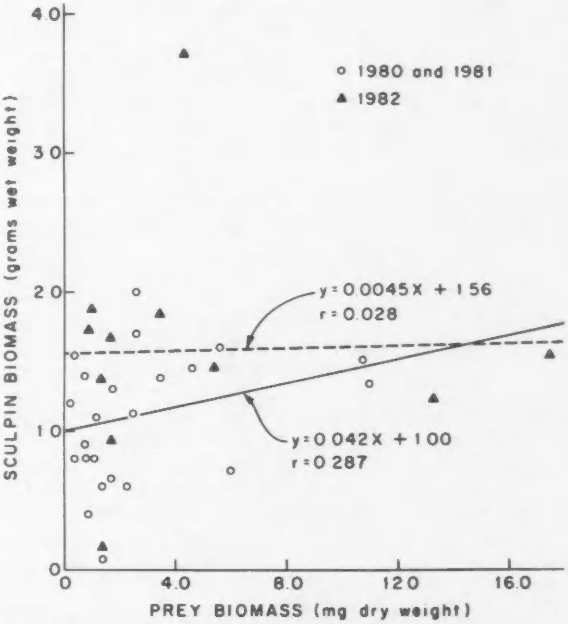

FIG. 1. Relationship between sculpin wet weight and dry weight of gut contents. Slopes of regression lines for 1982 data and for 1980 and 1981 data were not significantly different from each other.

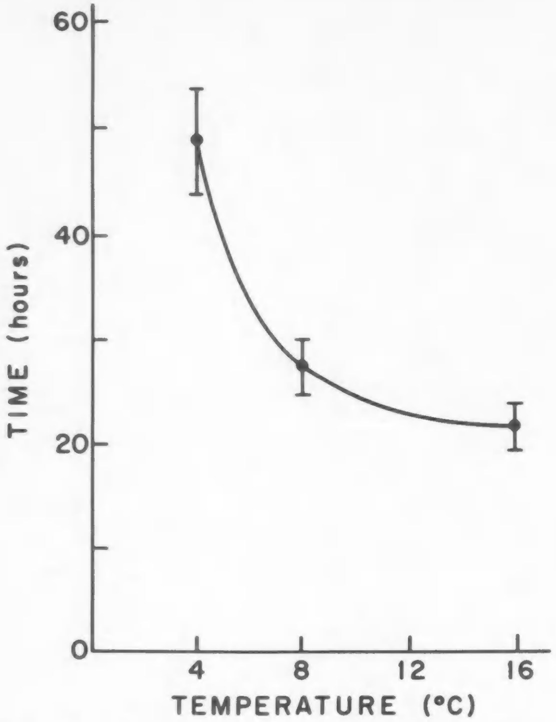

FIG. 2. Sculpin gut passage times are shown for 4, 8, and 16°C. Vertical bars are ± 1 SE of the mean.

slopes of the regressions did not differ significantly ($t = 0.515$, df = 32, $p > 0.5$). The overall regression of sculpin wet weight and prey dry weight was

$$W = 0.032P_W + 1.15 \quad r = 0.201.$$

The slope of this regression equation was not significantly different from zero ($t = 0.915$, df = 35, $p > 0.3$).

Sculpins digested *Heterotrissocladius*, *Stictochironomus*, and *Procladius* larvae at similar rates. After 5 d of eating the standardized diet of the three prey types, the five sculpins had completely digested 76.0 ± 6.1% (mean ± SE) of *Heterotrissocladius*, 78.8 ± 7.3% of *Stictochironomus*, and 80 ± 7.1% of *Procladius*. These percentages were not significantly different from each other ($F = 0.072$, $p \gg 0.75$). Similarity in digestion rates of the three prey types permitted us to use *Heterotrissocladius* as a fecal marker to measure gut passage of the ration prey, *Stictochironomus*.

Sculpin gut passage times decreased with increasing temperature (Fig. 2). The rate of gut passage was fitted to the exponential decay equation, such that

$$\ln R = 0.065T - 4.00 \quad r = 0.74.$$

A slightly better fit was given by a quadratic model:

$$R = 163.07T^{-2} + 13.84 \quad r = 0.82.$$

For both models, the correlation coefficient was highly significant ($p < 0.001$, df = 21); thus, both models adequately describe the rate of gut passage as a function of temperature over the range of temperature studied.

Discussion

The natural diet of slimy sculpins in Toolik Lake consisted almost entirely of chironomids. The genera of chironomid larvae that occurred in sculpin guts were representative of the chironomid genera in the soft sediments of Toolik (Hershey 1983, 1985a), with the exception that *Stictochironomus* accounted for only 12.4% of the items found in the gut (Table 1), whereas it was usually the most abundant chironomid in benthic samples (Hershey 1985a). It may have been less available to sculpins because it burrows deeper beneath the sediment surface than other chironomids in Toolik (Hershey 1985b). Van Vliet (1964) also suggested a similar mechanism for lack of feeding on *Chironomus* by the sculpins in Lac la Ronge. *Stictochironomus* is also more abundant in macrophytes, and sculpins forage more efficiently in bare sediments (Hershey 1985b).

As shown in Fig. 1, dry weight of sculpin gut contents did not increase with sculpin size. This is probably due to the shortage of prey taxa larger than chironomid larvae in Toolik Lake. Thus, Toolik Lake sculpins may be food limited, at least as they get larger. Toolik Lake sculpins live longer than other populations that have been studied, but reach a smaller maximum size (McDonald et al. 1982). Van Vliet (1964) found that sculpin size was related to food supply. Sculpins apparently have minimum size requirements for reproduction (Van Vliet 1964; Craig and Wells 1976). McDonald et al. (1982) found an exponential increase in mortality of Toolik sculpins after age IV, the presumed onset of reproduction. However, they found little mortality in sculpin age classes I–IV. Thus, the chironomid dominated benthic community may be a favorable food resource for small, nonreproductive sculpins, but may severely limit survivorship of reproductive-sized sculpins.

Although gut passage was considerably slower at 4°C than at typical summer temperatures, it did not occur at an insignificant rate (Fig. 2). Van Vliet (1964) found a similar digestion rate at 3°C for sculpins collected from the Montreal River. He also found that sculpins had fullest guts during the winter, and that they feed most at night. Broadway and Moyle (1978) found that sculpin feeding was not dependent on light. Arctic winters are dark and cold, and most biological activity is assumed to cease or slow to an insignificant pace during the winter. This may not be true of sculpin feeding on chironomids. Sculpins appear to digest food about twice as quickly at summer temperatures than at winter temperatures (Fig. 2), but sculpins experience winter temperatures (2.5–4°C) for three times as long (M. C. Miller, University of Cincinnati, Cincinnati, OH, pers. comm.). If sculpins feed in the winter at a rate corresponding to their digestion rate at winter temperatures, the potential impact of sculpins on chironomid densities during the winter would be 1.5 times as great as the potential impact in the summer. In a 3-wk exclosure experiment in the summer, sculpins reduced chironomid density in bare sediments by about 34% (Hershey 1985b).

Winter feeding may be an even greater stress on chironomid populations, however, because sculpin density in the soft sediments of Toolik is higher during the winter than in the summer. In the summer the sculpin population is spread out between the rocky and soft-sediment areas of the littoral zone (McDonald et al. 1982). However, the rocky littoral area is frozen during the winter, and sculpins must migrate to the deeper soft-sediment areas. Sculpin density in the rocky littoral area ranges from 0.44 to 2.58 sculpins/m^2 (McDonald et al. 1982). The only available estimate for the soft sediments is 1.08 sculpins/m^2 (McDonald et al. 1982). Assuming approximately the same average sculpin density in the two habitats, and considering that 25% of the lake area is rocky, sculpin winter density would be 33% higher in the sediments than summer sculpin density.

Sculpins are the only fish in Toolik Lake that eat larval chironomids, and larval chironomids, together with snails and clams, comprise most of the benthic fauna (Cuker 1981; Hershey 1983). Sculpins are often important in the diet of lake trout (Van Oosten and Deason 1938; Rawson 1961; Moyle 1977; Marten and Olver 1980) and burbot (Van Oosten and Deason 1938; Scott and Crossman 1973). If sculpins are important in the diet of these fishes in Toolik Lake, they may play a major role in cycling benthic production into the water column, and thus may be central to the trophic dynamics of the lake.

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Swimming Performance and Behavior of Rainbow Trout (*Salmo gairdneri*) and White Perch (*Morone americana*): Effects of Attaching Telemetry Transmitters

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Implicit in biotelemetry studies is the assumption that transmitter attachment does not affect fish behavior or performance. We conducted experiments to determine effects of external, surgical, and stomach tag attachments on the swimming performance and behavior of rainbow trout (*Salmo gairdneri*) and white perch (*Morone americana*). Only one rainbow trout changed dominance rank after dummy tag attachment. Subordinate fish had significantly lower weights than subdominant and dominant fish, but there were no significant differences in exhaustion times. Externally tagged trout had significantly lower exhaustion times than other tagged groups and controls. There was no significant difference in exhaustion times among tagged white perch and controls. Externally and surgically tagged perch contracted serious fungal infections during a 45-d survival study; however, few disease and no survival problems among tagged and untagged rainbow trout were noted up to 21 d. With all factors taken into account, it appears that stomach tagging is the best method of transmitter attachment, except when regurgitation and/or stomach atrophy are likely to be encountered.

Dans les études biotélémétriques, il est sous-entendu que la fixation de transmetteurs n'influe pas sur le comportement ou la performance des poissons. Les auteurs ont mené des recherches afin d'évaluer l'incidence d'étiquettes, fixées à la surface, par chirurgie et dans l'estomac, sur la performance natatoire et le comportement de la truite arc-en-ciel (*Salmo gairdneri*) et du bar-perche (*Morone americana*). Seule une truite arc-en-ciel a changé de rang de dominance après la fixation d'une fausse étiquette. Les poissons subalternes étaient significativement moins lourds que les sous-dominants et les dominants, mais il n'y avait aucune différence significative entre les temps d'épuisement. Ceux-ci étaient significativement moins élevés chez les truites portant des étiquettes externes que chez les autres groupes étiquetés ou les groupes témoins. Il n'y avait pas de différence significative entre le temps d'épuisement chez les bars-perches étiquetés et chez les témoins. Les bars-perches portant des étiquettes externes et des étiquettes fixées chirurgicalement ont contracté de graves infections fongiques au cours d'une étude de 45 jours sur la survie ; toutefois, peu de cas de maladies et aucun problème de survie n'ont été notés chez les truites arc-en-ciel étiquetées ou non pendant les 21 premiers jours. Quand on considère tous les facteurs, il semble que l'étiquetage stomacal soit la meilleure méthode de fixation d'un transmetteur, sauf dans les cas possibles de régurgitation ou d'atrophie de l'estomac.

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Use of biotelemetry to monitor fish in their environments has increased since the introduction of ultrasonic tracking (Trefethen 1956). Transmitter attachments influence behavior and performance, but the extent is uncertain and variable. Most evaluations of tagging effects are derived from anecdotal field observations made while studies are in progress. Reported effects often appear to be species, habitat, size, or method specific, or an interaction of factors (Haynes and Gray 1979).

In reviewing underwater biotelemetry, Stasko and Pincock (1977) reported that over 40 fishes have been studied, but concluded controlled studies on transmitter effects were lacking. Effects observed in recent controlled studies include decreased swimming speed by externally tagged and impaired performance by smaller stomach tagged Atlantic salmon (*Salmo salar*) smolts (McCleave and Stred 1975), abnormal post-recovery behavior in the field by surgically tagged Guadelupe bass (*Micropterus treculi*) (Manns and Whiteside 1979), greater weight loss among surgically tagged saugers (*Stizostedion canadense*) but no differences in mortality (Wrenn and Hackney 1979), failure of stomach tagged chinook salmon (*Oncorhynchus tshawytscha*) to migrate past hydroelectric dams (controls and externally tagged salmon performed equally well) (Haynes and Gray 1979), and reduced spontaneous activity and avoidance/pursuit behavior by surgically and externally tagged rainbow trout (*Salmo gairdneri*) (with external tags more disturbing) (Zimmerman 1980).

Transmitter attachments can adversely affect fish, thus biasing field data. Researchers must clearly understand the potential advantages and disadvantages each attachment method may

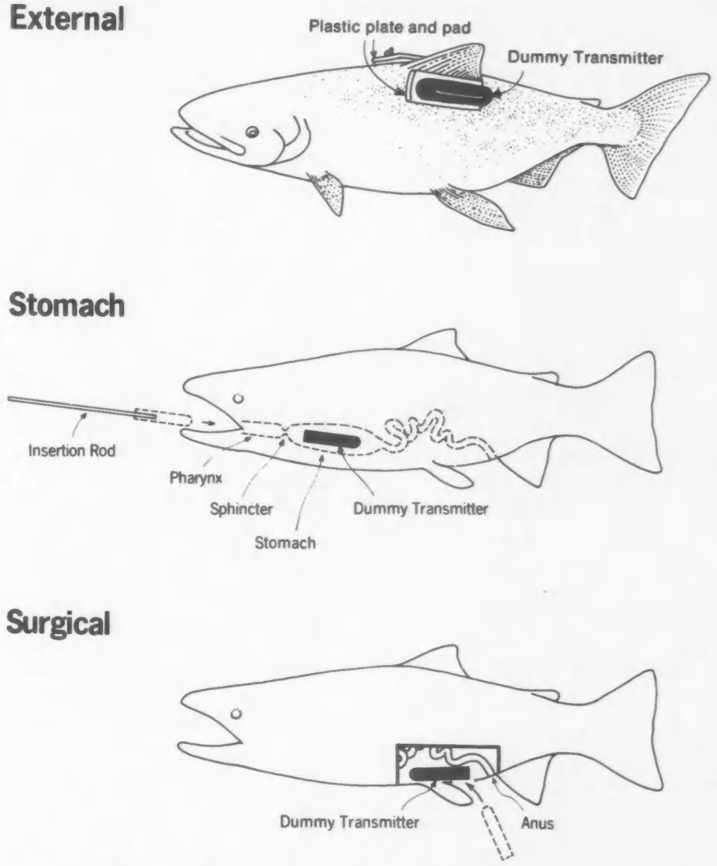

FIG. 1. Dummy transmitter attachment methods.

have on fish movement and behavior. To this end we conducted controlled laboratory experiments designed to evaluate the effects of external, surgical, and stomach transmitter attachment methods on swimming performance and behavior of two freshwater fish species with very different physiological, behavioral, and habitat characteristics: rainbow trout and white perch (*Morone americana*).

Materials and Methods

From February through May, four separate groups of rainbow trout (80 total) were transported from the New York State Department of Environmental Conservation Fish Hatchery at Caledonia, NY, to our laboratory. They were randomly assigned to 500-L flow-through tanks in groups of four. Trout length and weight ranged from 24.5 to 30.5 cm and 168 to 372 g. Based on four 10-min observations daily, each trout was given one of three rankings: dominant, subdominant, or subordinate. Agonistic displays (frontal and lateral threat displays, nipping, and posture), fight displays (pushes and bites), plus feeding and territorial responses distinguished ranks. After 1 wk, trout were anesthetized (tricainemethanesulfonate-quinaldine) and randomly tagged using one of four treatments: control (handled, but no tagging), external, surgical, or stomach (15 fish per tag type).

Cylindrical dummy transmitters (1.0-cm diameter) were constructed of epoxy resin and averaged 2.9 ± 0.2 cm and 3.0 ± 0.2 g. Transmitter size, shape, and weight simulated proportions commonly used in the field and did not exceed 1.7% of a fish's body weight. Transmitters were attached externally with a side-saddle harness (Fig. 1) in about 2 min. Using a needle, attachment wires passed through a rubber pad, the fish, and a rubber pad/plastic plate opposite the transmitter. Half-hitches secured wires to plastic plates. Surgical implantation was accomplished in about 4 min by opening a 2-cm incision between the pelvic fins and the anus (Fig. 1). A sterilized (alcohol) transmitter was inserted into the coelom and the incision was closed with 2.7-kg-test monofilament line. Stomach insertion was the easiest of the three attachment methods (Fig. 1) and required about 30 s. A glass rod fitted snugly into the hollowed end of a sterilized transmitter was dipped in glycerin and pushed down the esophagus into the stomach. Disinfectant was applied externally to punctured tissue.

After revival (~5 min), fish were returned to original aquaria. Dominance behavior was observed for another week, then trout were selected randomly for swimming tests. Feeding (commercial trout pellets) stopped 24 h before testing. Exhaustion times were measured in a circular rotating chamber (McCormack 1980), based on modified designs of Fry and Hart (1948), Bainbridge and Brown (1958), Boyar (1961), and Mellas (1982). A

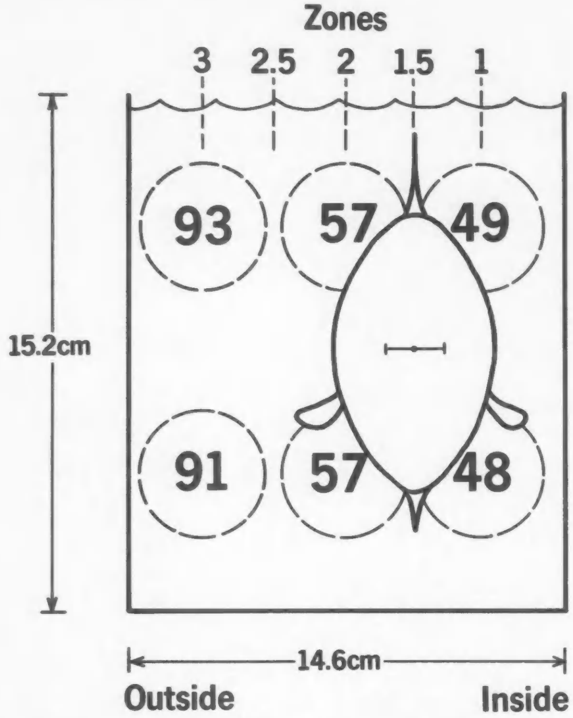

FIG. 2. Cross section view of the swimming chamber. The fish cross section represents the relative size and mean horizontal swimming position (1.54 ± 0.04) for rainbow trout. Numbers in circles are the final current speeds for rainbow trout 15 cm downcurrent from the front screen of the fish retaining cage, 2 cm above bottom and 2 cm below the surface. To create exhaustion time correction factors for fish position during swimming tests, the chamber was divided visually into five zones: 1, 1.5, 2, 2.5, and 3. Fish position was recorded for each minute during a test. Correction factors were computed by dividing the mean test position of individual fish by the mode test position for all fish (1.5 for 91% of observations). Correction factors reduced exhaustion times for fish swimming in slower currents nearer the inner wall and raised times for fish swimming in higher currents nearer the outer wall (e.g. for a fish with an average position of 1.38 and exhaustion time of 22 min, the adjusted exhaustion time was 1.38/1.5 × 22 = 20.2 min).

stationary wire mesh cage held fish in position relative to the current. A variable speed motor changed current speeds during tests (Mellas 1982). Current speeds and variations at each motor setting were determined with a pigmy flowmeter. There were few differences between speeds 5 and 15 cm down-current from the front retaining screen or between 2 cm above the bottom and 2 cm below the surface. However, major differences existed across the width of the trough. These were corrected (explained in Fig. 2).

Based on a pilot study, the current regime shown in Table 1 was used to determine rainbow trout exhaustion times. Individual trout were placed into the stationary retaining cage with the water moving at 39 cm/s. Fish adjusted for the specified acclimation periods before the current was increased to the final test speed of 57 cm/s. This speed was maintained for 30 min or until final exhaustion, recorded as minutes until exhaustion, at 57 cm/s. Final exhaustion was defined as inability to swim away from the rear screen of the retaining cage after receiving two 1-s shocks (0.5 A, 4 V) in a 30-s period.

Water temperatures between 9 and 12°C and dissolved oxygen levels were maintained by siphoning fresh water into the chamber and by placing iceblocks in the central hub of the swimming chamber. Oxygen concentrations ranged from 10.1 to 11.3 mg/L at 12°C (Winkler titration, American Public Health Association 1976), representing a minimum of 97% saturation.

From June through August, four separate groups of white perch (120 total) were electroshocked and transported from Lake Ontario to the laboratory. Pilot studies revealed no dominance behavior in white perch (19.0–31.5 cm, 106–635 g), so tagging commenced 48 h after arrival. No tag weighed more than 2.8% of a perch's body weight. With minor exceptions tagging was the same as for trout (Fig. 1). Small patches of ctenoid scales were removed before external and surgical attachments to ease surgical penetrations. This procedure lengthened attachment time for external tags to approximately 2.5 min and surgical tags to approximately 5 min. White perch required 10–15 min to revive from anesthesia. After tagging, white perch were held 24 h and then randomly tested (25 fish per tag type) in the swimming chamber using a current regime derived from a pilot study (Table 1). Temperature (20–23°C) and dissolved oxygen were maintained by adding fresh water during tests. Upon completion of swimming tests, white perch in the first three groups returned to the laboratory were immediately killed and sexed. Individuals in the last group were held up to 45 d to examine longer term transmitter effects. They were fed a variety of foods twice daily, including trout pellets, frozen brine shrimp, salmon filets, and live minnows. As perch died or at the end of the 45-d period, a necropsy was performed to examine external and internal attachment sites.

Statistical examinations were by two-way ANOVA (exhaustion time/dominance and weight/dominance for rainbow trout and sex/exhaustion time for white perch) and linear regression, unless otherwise indicated. The significance level used was $\alpha = 0.05$. Because of the high correlations between length and weight for trout and perch, only weight was used in analyses (Mellas 1982).

Results

Rainbow Trout

Erratic swimming behavior inside the swimming chamber was almost nonexistent. Within 1 min after placement into the chamber, trout aligned themselves against the current and remained there until fatiguing and finally lying against the rear retaining screen, unable to swim away despite shocks. Rainbow trout also appeared unaffected by the strong velocity gradient across the chamber. Fish generally positioned themselves in the slowest currents available to them (Fig. 2). Whenever a fish moved into faster water near the outer wall, it began to fall back in the retaining cage, increased swimming speed momentarily, then gradually resumed position near the front retaining screen and inner wall. There was no significant difference ($P > 0.25$) in weight among tagged groups (Table 2), nor was there a significant relationship between weight and swimming performance ($r^2 = 0.014$).

There was no significant difference ($P > 0.5$) in exhaustion times among dominance ranks (Table 2). Although subordinate fish were submissive and appeared weaker in the presence of dominant fish, they and subdominants performed as well as dominants when isolated in the swimming chamber. There was, however, a highly significant difference ($P < 0.001$) in exhaus-

TABLE 1. Current speeds and times used in rainbow trout and white perch swimming tests.

Acclimation (min)	Speed (cm/s)[a]
Rainbow trout	
3	39
3	47
30	54
30[b]	57
White perch	
3	39
3	43
20	47
30[b]	51

[a] Top–middle location, 15 cm downcurrent from front screen (Fig. 2).

[b] Or until exhausted; 59 of 60 trout and all 100 perch succumbed to exhaustion within 30 min.

TABLE 2. Weights and exhaustion times of rainbow trout (by tag type and dominance rank) and white perch (by tag type and sex).

Group	N	Weight (g) ($\bar{x}$ ± SD)	Exhaustion time (min) ($\bar{x}$ ± SD)
Rainbow trout			
Dominant	21	277±34	20.0±5.2
Subdominant	14	268±27	18.9±5.7
Subordinate	25	230±35	19.1±5.4
Control	15	252±35	22.3±4.1
External	15	257±37	13.5±4.0
Surgical	15	252±47	19.8±4.5
Stomach	15	261±41	21.8±3.8
White perch			
Male	39	198±69	12.9±5.0
Female	61	295±137	10.1±5.2
Control	25	266±132	10.3±5.3
External	25	262±109	11.7±5.5
Surgical	25	255±134	10.3±4.7
Stomach	25	244±127	12.4±5.5

tion times among tagged groups, with externally tagged fish having shorter exhaustion times (Table 2) than other tagged groups (least significant difference test). Interactions between dominance and tag type were not significant ($P > 0.5$).

We observed dominance–subordination relations among rainbow trout before and after tagging (cf. Stringer and Hoar 1955; Newman 1956; Jenkins 1969; Chiszar et al. 1975). Only one trout changed rank after tag attachment (stomach treatment from dominant to subordinate). However, there was a highly significant difference ($P < 0.005$) in weights (Table 2), with subordinate fish weighing significantly less than dominants and subdominants (least significant difference test). The strong correlation between large body size and dominance in our trout is well documented for many salmonid species (Kalleberg 1958; Hartman 1963, 1965). There was no significant interaction between dominance ranks and tag types ($P > 0.5$).

Noticeable behavioral alterations, independent of fish dominance, resulted from tag attachment. Irregular swimming increased in externally tagged trout, with quick, darting movements and occasional substrate scraping appearing to be efforts to dislodge the tag. During one feeding session the saddle of one externally tagged trout tangled in a floating thermometer. The thrashing that followed suggested a clear drawback to external tag attachment: possible entanglement in the environment. Rainbow trout with stomach tags were clearly discomforted. Increased flaring of the gill opercula and coughing behavior were observed frequently. Of stomach-tagged trout, 80% regurgitated the tag at least once in 2 wk; one regurgitated its tag seven times in 10 d. Regurgitated transmitters were reinserted underwater, without anesthesia, following Koo and Wilson (1972). Surgically tagged trout exhibited no noticeably changed behaviors.

White Perch

Positive rheotaxis in white perch was not nearly as strong as it was in rainbow trout, and in some fish was not observed until the highest water velocity was achieved. Their awkward, variable, and nonrhythmic swimming style made accurate measurement of swimming performance more difficult, and variability was quite high.

Most of the perch collected, especially in earlier test groups, were gravid, corresponding with their spawning season in Lake Ontario (Scott and Crossman 1973). Gravid females were noticeably less streamlined than smaller males, suggesting that greater swimming effort was required for females. However, there was no significant swimming performance differences between sexes ($P > 0.25$) or among tagged groups ($P > 0.5$), nor was there a significant interaction ($P > 0.10$). There was little relationship between exhaustion time and weight ($r^2 = 0.152$).

Of the 17 white perch held for long-term studies (4 external, 6 stomach, 4 surgical, and 3 control), 9 ate regularly, 3 ate occasionally, and 5 did not eat (2 control, 1 external, 1 stomach, and 1 surgical). Seven fish died before the end of the 45-d period (3 surgical, 2 external, 1 stomach, and 1 control).

A common long-term effect of external transmitters was severe muscle damage caused by attachment wires. The initial penetration hole had enlarged up to 1 cm in diameter, causing the external saddle harness to loosen considerably, but none of the transmitters were lost. Additional dorsal scales were missing and dorsal musculature deterioration was evident, as were fungal infections in three externally tagged fish.

Regurgitation of stomach tags occurred in only two white perch (8%). Visual examination revealed no apparent digestive tract damage, with tags appearing securely settled in perch stomachs. Stomachs coloration and muscle tone and texture were not visably different from perch receiving other treatments. Although transmitters occupied about 80% of the total volume of an empty stomach, their presence did not prohibit feeding. Digested food was found in the stomach and intestines of regularly feeding stomach-tagged fish (five of six), indicating no digestive tract blockage.

Sutures used to close the ventral incision made during surgical implantations remained secure during the long-term study. Incisions appeared to heal well, although external fungal infections developed in three fish and two died within 10 d after testing. Necropsy revealed that transmitters were located farther anterior within the coelomic cavity than where initially placed. Internal organ damage caused by transmitter placement or movement was not evident, although intestinal damage from the initial incision was discovered in one fish that died 2 d after surgery. Fatty tissue was deposited around all four surgically implanted transmitters, with the largest amount encapsulating the entire tag in one fish that survived the 45-d test period.

Discussion

Swimming performance by fishes has been widely studied (cf. Hoar and Randall 1978 for a complete review) using a variety of devices (cf. Olofsson and Lindahl 1978; Bainbridge 1958, 1962; Boyar 1961; Blaxter and Dickson 1959; Brett et al. 1958). While stamina tunnels using pumped, laminar flow water are preferred for obtaining precise physiological and performance measures (as opposed to circular, rotating chambers), we compared telemetry attachment methods under controlled conditions and did not evaluate swimming performance per se.

The strong swimming performance of rainbow trout was not surprising given their abundant red muscle and migratory habits. Nor was the weak swimming performance of white perch unexpected, given their relative lack of red muscle and lentic habitat. While external transmitters clearly reduced swimming ability in rainbow trout, high regurgitation rates for stomach transmitters and greater risks associated with surgical attachments make choosing a single best attachment method difficult for rainbow trout (and probably salmonids generally) and dependent upon what information is desired and a fish's habitat. If swimming speed and endurance are not critical, external attachment may be appropriate. For white perch, external and surgical attachments were clearly disadvantageous over extended times, but stomach insertion appeared to create no difficulties. For white perch (and perhaps other spiny rayed and/or white muscled fishes), stomach insertion appears to be a better attachment method. Also, rainbow trout apparently tolerated handling much better than white perch (as evidenced by more widespread and severe fungal infection in perch). Stomach tagged perch may have survived better because they were handled less. Therefore, handling time and severity may strongly influence tag choice.

External tags appear to impair swimming performance more in fusiform, lotic fishes (McCleave and Stred 1975). Nonfusiform shape and/or less exposure to constant currents in lentic or pelagic fishes may minimize impaired performance resulting from external tags. However, the extent of reduced performance under field conditions may differ, since fish can select among different current speeds. Swimming delays have been reported for externally tagged fish (Stasko et al. 1976; Haynes and Gray 1979). Increased drag from external transmitters (Haynes 1978) may cause fish to reduce or discontinue swimming, especially in high-speed currents (i.e. riffles, fish ladders, raceways).

Association with vegetation and/or structure increases entanglement risks and may determine whether external transmitter attachment is suitable. Although no external transmitters were lost during our experiments, other studies have reported losses in the field (Haynes and Gray 1979; Nettles 1983; and K. Parnell, Department of Biological Sciences, SUNY College at Brockport, pers. comm.) Substrate scraping, like that observed in our externally tagged rainbow trout and in white sturgeon (*Acipenser transmontanus*) (Haynes 1978), probably causes external tag loss.

Surgically tagged fish performed equally as well as control fish in swimming tests, but other studies indicate that surgical attachment may (Henderson et al. 1966; Stasko et al. 1973; Nettles 1983) or may not (Dodson and Leggett 1973; Warden and Lorio 1975) affect performance in the field. Surgical attachment has the advantages of lying near a fish's center of gravity, not being lost or entangled in the environment, and not creating drag forces while swimming. Despite these advantages, the most serious adverse effects of transmitter attachment in our studies appeared in surgically tagged fish. Surgical attachment required the most handling, anesthesia, and revival time and resulted in the most widespread and serious infections (75% perch; 20% trout).

Similar adverse responses to surgical attachment have been observed in the field. To allow for fuller recovery from tagging and anesthesia, surgically tagged rainbow and brown trout (*Salmo trutta*) were held for up to 24 h before release into Lake Ontario (Nettles 1983; K. Parnell, pers. comm.). Despite this precaution, approximately one third of these trout apparently died within 14 d after release, compared with no confirmed mortalities for externally tagged trout. In fact, immediate release after recovery from anesthesia has proved far more effective for steelhead (K. Parnell, pers. comm.) and Pacific salmon (C. Keleher, Department of Biological Sciences, SUNY College at Brockport, pers. comm.).

Although laboratory conditions appeared ideal for safe recovery from surgery, infection and death still resulted. To insure the health and survival of tagged fish after release into the environment, reasearchers should use surgical attachment of telemetry devices with caution, especially in small fish and spawning or otherwise weakened fish.

Scale type should be considered before attaching or implanting telemetry devices. The removal of large ctenoid scales in white perch to facilitate penetrations increased handling time and resulted in fungal infection, muscle deterioration, and ultimately death in many perch. Although attachment did not affect swimming performance 24 h after tagging, performance would have been affected days or weeks later. None of the adverse effects observed in white perch appeared in rainbow trout after 21 d, indicating that different species do not accept external attachments equally well, especially when scale types and muscle tissues differ.

Successes with stomach tagging have been reported in field studies (Henderson et al. 1966; Yuen 1970; Groot et al. 1975), but other studies have reported adverse effects (Dodson et al. 1972; Haynes and Gray 1979). Stomach tagging did not reduce fish swimming performance and resulted in no infections or deaths in our study. None of the white perch necropsied showed signs of stomach rupture, internal organ damage, or digestive tract blockage. Reduced feeding resulting from stomach insertion in rainbow trout and white perch was not evident.

Stomach insertion has the same advantages as surgical tagging in addition to being very quick and not requiring body penetrations. One potential drawback is regurgitation of tags. Most stomach-tagged rainbow, but only two white perch, regurgitated transmitters, indicating that two similarly sized, taxonomically different species do not necessarily retain stomach insertions similarly. Depending on species, regurgitation may (Stakso and Rommel 1974; Kelso 1976; McCleave et al. 1978) or may not (Koo and Wilson 1972; Kelso 1974; Groot et al. 1975) occur in the field.

In conclusion, by testing two species with very different life histories and habitats, we identified some physiological, behavioral, and ecological constraints to be considered before attaching telemetry devices to fish. With all factors taken into account, stomach insertion represents the best method of transmitter attachment, except when regurgitation or stomach atrophy are likely to be encountered. Then one must choose between surgical and external methods, depending on the balance of fish habitat and physiology constraints and the objectives of a study.

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Introduction to Limnological Research at Saqvaqjuac, Northern Hudson Bay

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Welch, H. E. 1985. Introduction to limnological research at Saqvaqjuac, northern Hudson Bay. Can. J. Fish. Aquat. Sci. 42: 494–505.

Saqvaqjuac, a Department of Fisheries and Oceans research site at 63°39′N, 90°39′W on the northwest coast of Hudson Bay, is described. Information is given on cultural history, geology, vegetation, climate, and lakes.

Le présent rapport décrit Saqvaqjuac, un site de recherche du ministère des Pêches et des Océans, situé à 63° 39′ N, 90° 39′ O sur la côte nord-ouest de la baie d'Hudson. L'auteur fournit des données sur l'histoire culturelle, la géologie, la végétation, le climat et les lacs.

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In response to the need for more detailed knowledge of arctic freshwater ecosystems, the Department of Fisheries and Oceans (DFO) (then Fisheries and Marine Service) Canada established a research camp at Saqvaqjuac.[1] Centered at 63°39′N, 90°39′W on the northwest shore of Hudson Bay about 40 km from the hamlet of Chesterfield Inlet (Fig. 1 and 2), the site was selected in 1976 because it is geologically similar to the Experimental Lakes Area (ELA) in northwestern Ontario; like ELA it has numerous small lakes suitable for experimental purposes; and logistically it gives the most arctic for the least money, being situated directly north of the Winnipeg–Churchill rail line with an annual sealift going into Chesterfield Inlet. The site is on an inlet of Hudson Bay, providing a protected waterway for small boat traffic during open water.

My purpose here is to outline the historical and geographical setting of the site, describe selected experimental lakes, and to provide an overview of the major research projects. Two papers, on winter circulation and respiration, follow this introduction, and a methane addition experiment was described by Welch et al. (1980); other reports will be submitted to the *Canadian Journal of Fisheries and Aquatic Sciences* as they are completed.

After tentative site selection, DFO personnel entered into discussions with the Chesterfield Inlet Settlement Council, and subsequently the Keewatin Inuit Association, about establishing the research camp. Local people expressed various concerns, DFO personnel presented the details of experiments as far as they were known, and agreement was reached regarding camp location and types of work to be done. Through these and subsequent meetings, the community was kept aware of events at Saqvaqjuac and minor misunderstandings were quickly corrected.

Considerable local employment was provided in the form of casual labor, summer students, cook and kitchen help, a permanent field technician, and a permanent camp maintainer. These people (and their families) enriched the lives of all, allowed researchers to view local resources from a resident's viewpoint, and provide skills which southern Canadians lacked.

Saqvaqjuac was first occupied by Department personnel in May 1977. By September, facilities included on-site electricity generation, shop, kitchen, laboratory, living quarters, a meteorological observatory, year-round running water provided by a siphon from a nearby lake, and a variety of transportation. The site is usually reached in winter by snowmobile and in summer by boat from Chesterfield Inlet. But during spring breakup (June and early July) and fall freezeup (approximately 1 October to approximately 10 December) the site is virtually inaccessible except by air. The terrain is too rough to allow wheeled aircraft landings at any time of year; float planes can land at the camp during July–September and wheeled/ski aircraft can land during October – early June on the sea or nearby lakes. Bulk resupply takes place in late summer by sea and in April by ski-equipped DC-3 aircraft from Churchill.

Cultural History

The northwest coast of Hudson Bay has likely been occupied continually for several thousand years, with probable Dorset and Thule remains on the shores of Saqvaqjuac Inlet (Wenzel 1971). The mouth of the Saqvaqjuac River (Fig. 2), undescribed in the archaeological literature, has been extensively occupied in the past. Remains of a sapotit (stone weir) used as recently as the 1960's (the late V. Sammuqtuq Sr., Chesterfield Inlet, pers. comm.) can still be seen at the head of the first rapids. On the adjacent plain on the northeast side of the river mouth, numerous caches, tent rings, graves, and kayak stands are found, while on the southwest side, in addition to all the above

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[1] Refers to the outer race that connects Saqvaqjuac Inlet with the main body of Hudson Bay. In Inuktitut, saqvaq = fast water or rapids and juac = big, large.

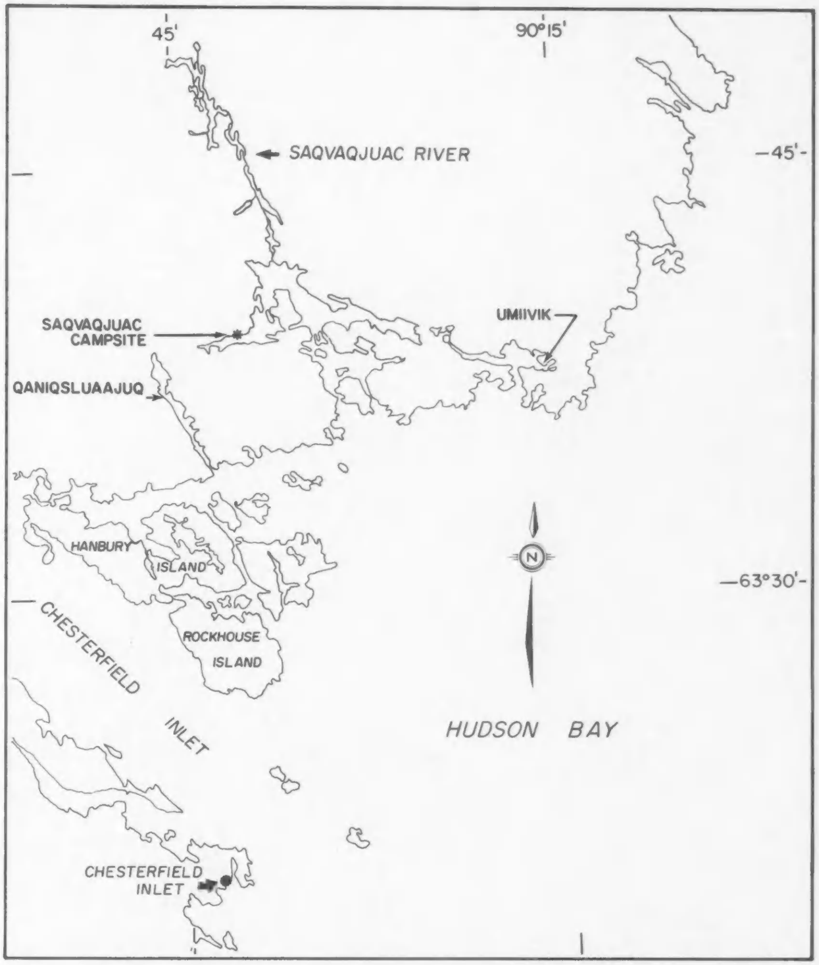


FIG. 1. Saqvaqjuac Inlet in relation to the northwest coast of Hudson Bay.

features, are several semi-underground winter dwellings dug into a sandy hillside. Tent rings are found everywhere in the Saqvaqjuac area.

Despite the obvious heavy usage of the area in earlier times, no Inuit have dwelt there permanently for several decades (the late J. Komaqsiutiqsaq, Chesterfield Inlet, pers. comm.), and today it is visited only by hunters, trappers, and families fishing for one to several days at a time. Visitors to the research camp are also frequent. Most travellers are from Chesterfield Inlet (population ≈ 280 people) or from Rankin Inlet (population ≈ 1000 people).

In historic times the nearby coastal areas were utilized by overwintering whalers and their associated native partners, and large numbers of musk ox, caribou, seal, walrus, and bowhead were taken, both for subsistence and for trade. The daily journal of Captain George Comer for 1903–5 (Ross 1984) is particularly interesting for its references to resource harvesting and contact with the Inuit in this area. The government of Canada first made its presence known in the area in 1903 when the *Neptune*, carrying Royal Northwest Mounted Police, geologist A. P. Low, and others, overwintered alongside Comer's ship *Era* at Cape Fullerton, about 90 km north of Saqvaqjuac (Low 1906). The arrival of the Roman Catholic Mission and the Hudson Bay Co. at Chesterfield Inlet in 1912, along with the police detachment, completed the establishment of twentieth century authority in the area.

Climate

Although Saqvaqjuac is at a relatively low latitude (south of the Arctic Circle, 66°N), it has a midarctic maritime climate, with an annual temperature range ≈ 65°C. Mean air temperature is about +10°C in July and −27°C December–March (Fig. 3). Mean daily wind speed is high, ≈ 21 $\mathrm{km \cdot h^{-1}}$ (Fig. 4), with no distinct seasonal patterns. The maximum 24-h mean wind speed recorded during 30 mo of observation was 51 $\mathrm{km \cdot h^{-1}}$, and the minimum was 3.4 $\mathrm{km \cdot h^{-1}}$. The site is well suited for wind-generated power although facilities have not been installed.

Meteorological records were kept at Chesterfield Inlet by the Department of Transport and Environment Canada from 1932 through 1980. The mean total annual precipitation is 29.13 cm. About 52% falls as rain during June–September, with the

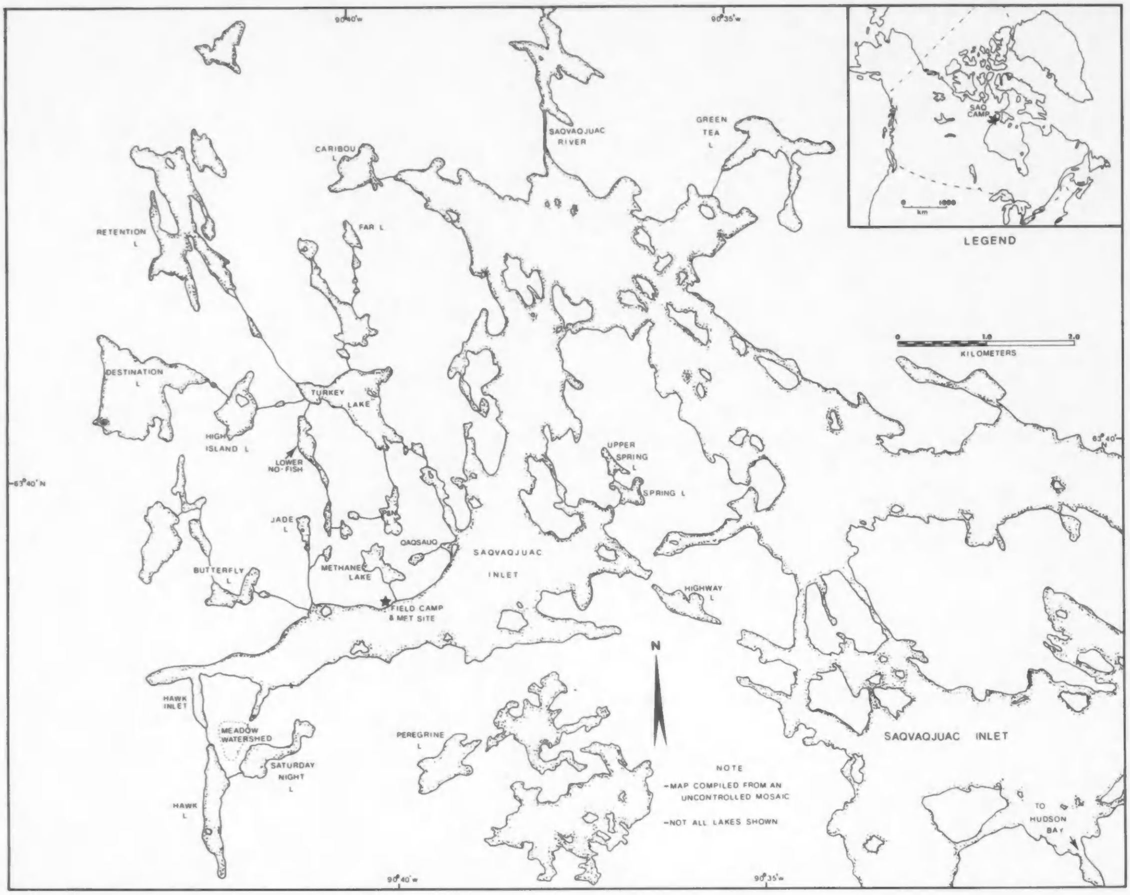

90°40'W
90°35'W
SAQVAQJUAC RIVER
GREEN TEA L
CARIBOU L
RETENTION L
FAR L
SAQ CAMP
0 1000 km
LEGEND
0 1.0 2.0
KILOMETERS
DESTINATION L
TURKEY LAKE
HIGH ISLAND L
LOWER NO-FISH
UPPER SPRING L
SPRING L
63°40'N
JADE L
QAQSAUQ
SAQVAQJUAC INLET
METHANE LAKE
BUTTERFLY L
FIELD CAMP & MET SITE
HIGHWAY L
N
HAWK INLET
MEADOW WATERSHED
SATURDAY NIGHT L
PEREGRINE L
HAWK L
NOTE
-MAP COMPILED FROM AN UNCONTROLLED MOSAIC
-NOT ALL LAKES SHOWN
SAQVAQJUAC INLET
TO HUDSON BAY
90°40'W
90°35'W

FIG. 2. Saqvaqjuac Inlet and selected nearby lakes.

remainder as snow during the winter (Fig. 5). Spring snowmelt runoff is precipitous and in dry summers may constitute nearly 90% of the total spring and summer runoff. In wet summers the runoff due to rainfall may be over 50% of total annual precipitation.

The area is underlain by about 300 m of continuous permafrost (Brown 1977), with an average active layer of ≈1 m in August (Dalton 1981). Fog is frequent on the open coast but occurs only occasionally at the camp site. No permanent snow fields occur in the immediate area.

Meteorological records for Saqvaqjuac are presented in Dalton (1981) and C. Allan and G. K. McCullough (in prep.).

Geology

Very little work has been published on the geology of the area northeast of Chesterfield Inlet; the following is extracted largely from Wright (1967) and Lee (1960). The area is underlain by granite, granitic gneisses, and granodiorite bedrock of Precambrian (Lower Proterozoic) age, K–Ar dated as 1.6×10^9 to 1.8×10^9 yr old. The pink granites contain quartz, biotite, hornblende, K-feldspar, and plagioclase, with some intrusions of gabbro or greenstone. Small outcrops of volcanic pillow lavas (greenstone) occur in the area, with veins of quartz, chlorite, and hornblende. Sedimentary and volcanic gneisses occur in the region of Saqvaqjuac Inlet, sometimes containing conglomeritic beds of various rock types (including rarely dolomite and limestones) and kyanite, garnet, and staurolite (Wright 1967).

The Keewatin glaciation scoured Saqvaqjuac bedrock in a southeasterly direction, and in recession (9000 – 10 000 yr B.P.) left glacial drift in low-lying areas, composed mostly of boulder–gravel deposits and a few areas of sandy–silt. In the immediate area of Saqvaqjuac Inlet, no large eskers, moraines, or drumlin fields are present. As the glacial ice receded to the Keewatin ice divide (along the axis Yathkyed Lake – Baker Lake – Wager Bay), glacially ice-dammed lakes formed to the west of the ice divide, in the Back, Thelon, Dubawnt, and Kazan River basins. To the east of the ice divide, seawater followed the melting ice into the Baker Lake region, and upon complete melting of the ice core, seawater moved up the Thelon River valley past the Keewatin western boundary and covered all land areas now occupied by Maguse Lake, Kaminak, and Kaminuriak lakes, Baker Lake, Armit Lake, and the lower half of the Lorillard River drainage basin. This Tyrrell Sea reworked and sorted the glacial deposits, and allowed the distribution of mussel shells and small deposits of marine silty clays over this region (Wright 1967). The Tyrrell Sea reached its maximum

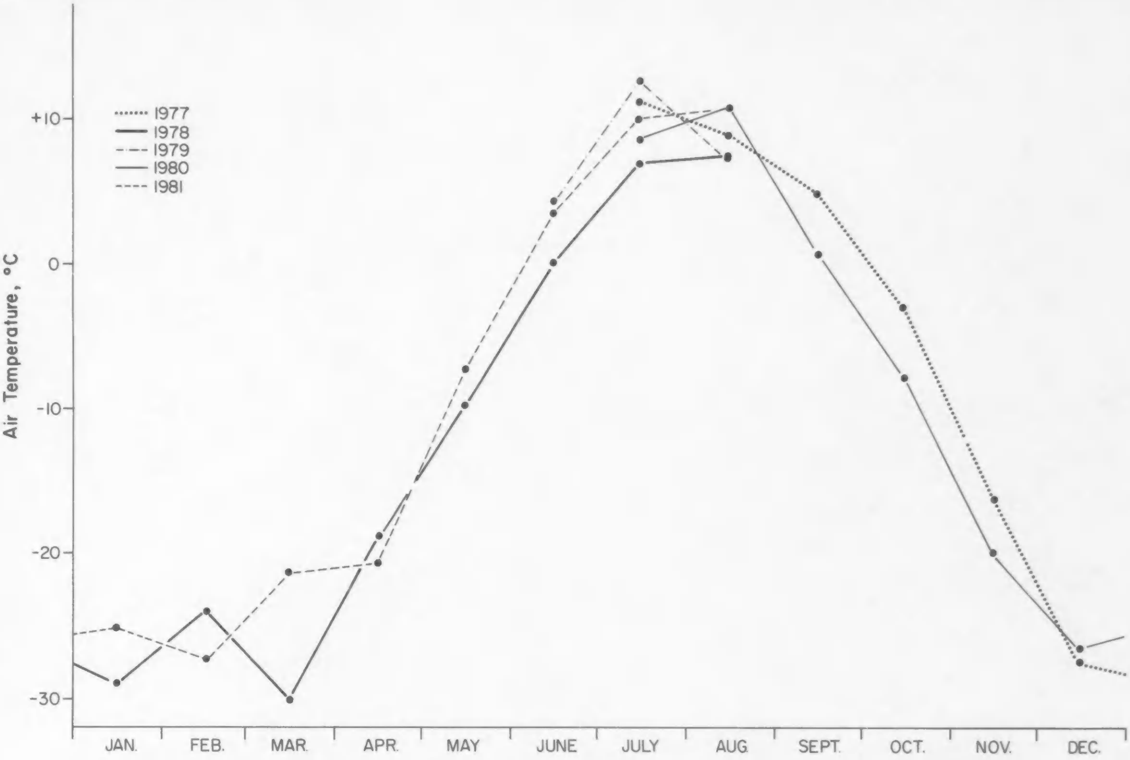


FIG. 3. Air temperature at Saqvaqjuac, taken as the mean of the daily maximum and minimum (Dalton 1981) by month.

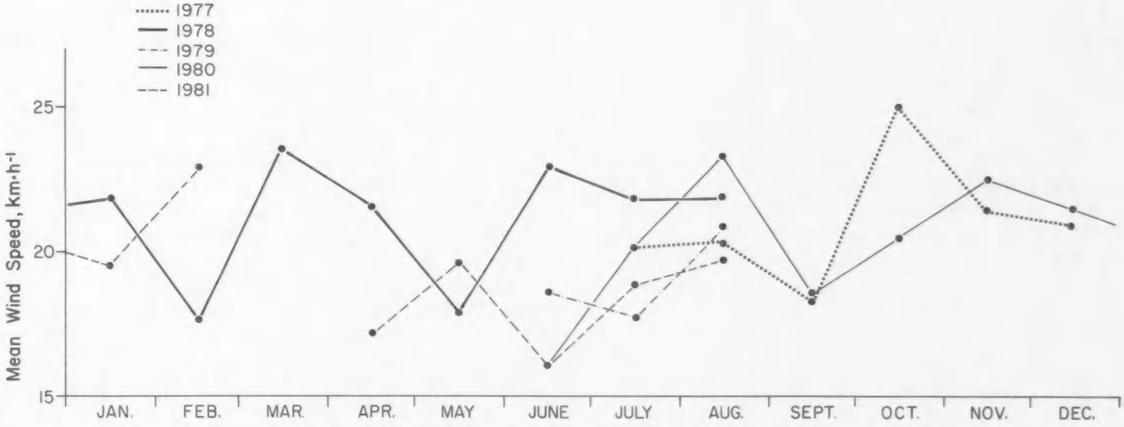


FIG. 4. Wind speed at Saqvaqjuac, taken as the mean of the daily wind run by month.

extent 7000–8000 yr B.P. (Lee 1960), and has been receding to the east up to the present time as a result of uplift of the land released from the weight of glacial ice.

As a result of this intensive glacial scouring and subsequent reworking of glacial deposits, Saqvaqjuac terrain is composed of innumerable hills of exposed gneissic bedrock (readily visible in Fig. 7), the upper portions of which have almost no till and which frequently show frost-heaved joint blocks (Washburn 1973). Gentle slopes are sparsely covered by soil. In the valleys are tills that support nearly 100% plant cover and that frequently show such periglacial features as unsorted circles and well-developed frost cracks (Fig. 7D).

Vegetation

Vegetation is typical barren-ground tundra, the needle-leaf treeline being about 350 km southwest at its closest. Various dwarf willow and birch species are abundant and exceptionally

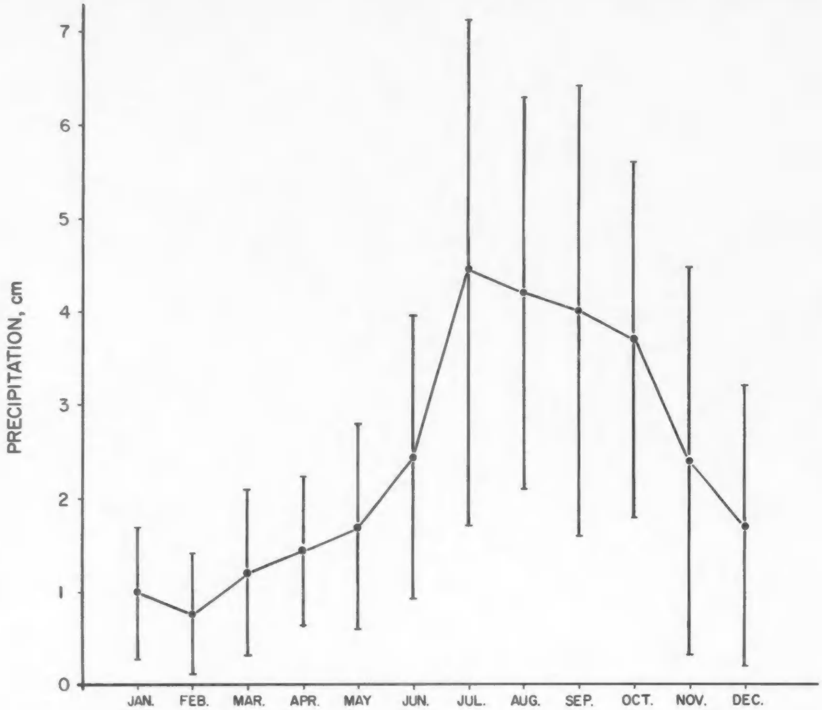


FIG. 5. Mean monthly precipitation at Chesterfield Inlet, based on Department of Transport and Environment Canada records from 1932 through 1980. (*Monthly Record Meteorological Observations*). Error bars are ± 1 SD.

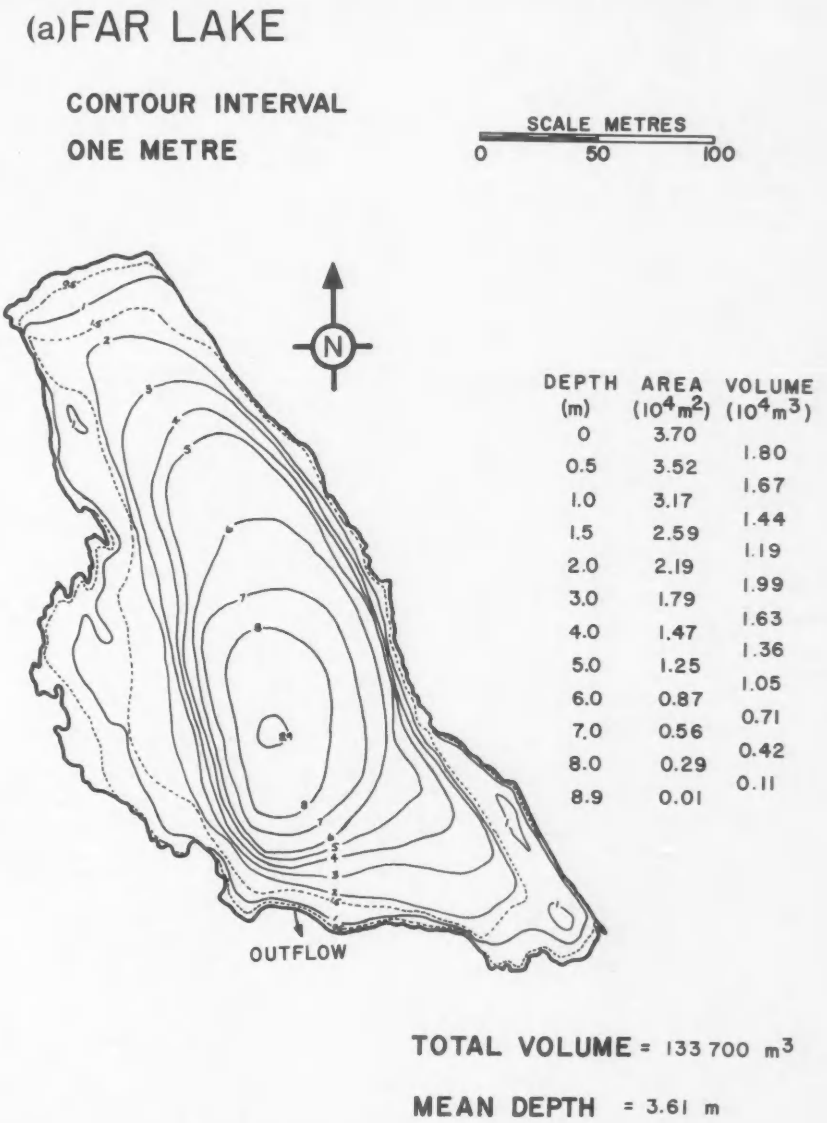
develop nearly continuous canopies 1–1.5 m high in protected areas where there is continuous running water from lake outflows. Wet meadows develop heavy growths of sedges (*Carex* spp.) and cotton-grass (*Eriophorum* spp.). Drier upland sites support a variety of low heaths (*Ledum, Empetrum, Andromeda, Pyrola, Vaccinium, Cassiope*) and tundra vegetation such as *Dryas, Hedysarum, Astragalus, Oxtropis*, several saxifrages, and on disturbed ground, *Epilobium latifolium*. Lichens are very abundant on all sites, with yellow-green and black wiry *Alectoria* spp. covering much of the exposed bedrock on hill tops. The moss, *Rhacomitrium*, forms mats in bedrock depressions. Vegetation is nearly continuous where till is present, except for the centers of frost boils, but the tops of hills and ridges hold till only in depressions and are thus largely devoid of vascular plants. Some shallow ponds (here defined as any water body that freezes to the bottom, <2 m maximum depth) support sparse margins of emergent vegetation, the rush *Hippurus*, and *Eriophorum scheuchzeri*.

Lakes

Lakes (here defined as water bodies that do not freeze to the bottom, $Z > 2$ m) are a conspicuous feature of the Saqvaqjuac landscape; about 17% of the land area shown in Fig. 2 is covered by lakes. Most are small, less than 50 ha, although 10–40 km to the north and east lie a number of lakes 1–10 km^2 in area. They all appear to be ice-scour lakes of glacial origin, where "... considerable area of very ancient uplifted land surface has been scoured by ice, which, as well as removing all loose material, has scooped out small rock basins in zones of fracture and along shatter belts." (Hutchinson 1957, p. 57). However, nearly all lake outlets are not bedrock controlled, but rather are dammed to varying degrees by glacial till, such that lake levels are higher than would be the case if the scoured basins held no glacial debris. To the south and west of Chesterfield Inlet the land surface becomes more rolling, with a more uniform cover of glacial till, and more lakes occupy drift basins formed as irregularities in ground moraine and as kettles.

The deepest lakes sounded in the immediate region have been Turkey (29 m) and Hawk (34 m), although extensive surveys have not been made. The lake basins have regular shapes with $\bar{Z}:Z_{\max}$ averaging about 0.38 (Table 1). Headwater lakes have low $A_d:A_0$, between 2 and 7 ($N = 6$; Table 1). Figure 6a–6g gives morphometry for the seven of the eight lakes that have been mapped in detail (after Dalton 1981). For Methane Lake, see Welch et al. (1980).

Saqvaqjuac lakes are nominally cold monomictic, circulating once annually July–September, although temporary stratification frequently occurs in midsummer (H. E. Welch and J. Legault, unpubl.). They freeze about 1 October and become icefree about 1 July, or as late as August for the largest lakes (10–50 km^2). The water is generally soft with low conductance (40–100 μS) and low total dissolved solids (15–30 mg·L^{-1}), although several lakes, notably Green Tea and Highway, have much higher conductances ($\simeq$400 μS) and obviously different biology, sustaining permanent blooms of *Anabaena*. Otherwise



DEPTH (m)	AREA ($10^4 m^2$)	VOLUME ($10^4 m^3$)
0	3.70	
		1.80
0.5	3.52	
		1.67
1.0	3.17	
		1.44
1.5	2.59	
		1.19
2.0	2.19	
		1.99
3.0	1.79	
		1.63
4.0	1.47	
		1.36
5.0	1.25	
		1.05
6.0	0.87	
		0.71
7.0	0.56	
		0.42
8.0	0.29	
		0.11
8.9	0.01	

TOTAL VOLUME = 133 700 m^3

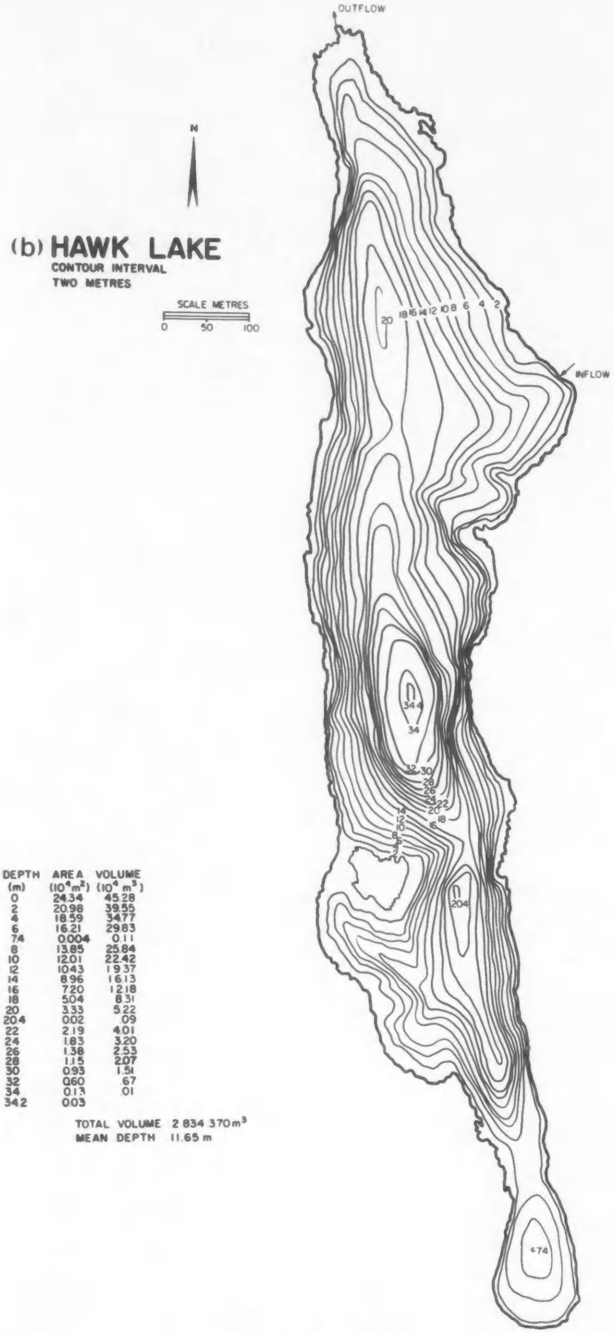
MEAN DEPTH = 3.61 m

FIG. 6. Morphometry of Saqvaqjuac lakes (continued next page).

the lakes are oligotrophic and clear, with Secchi depths typically 5–10 m in summer.

Deep lake sediments are fine-grained, with 10–30% loss on ignition. A conspicuous margin of light-colored (not sediment-covered) rock and gravel exists around the shores and extends to ≈2 m depth, the depth of maximum ice development. Thus, the area of nonfrozen lake can easily be seen from aerial photographs, especially those in color (Fig. 7). Ponds lack such margin developments; typically, pond bottoms appear uniform from shore to shore when viewed from the air (Fig. 7).

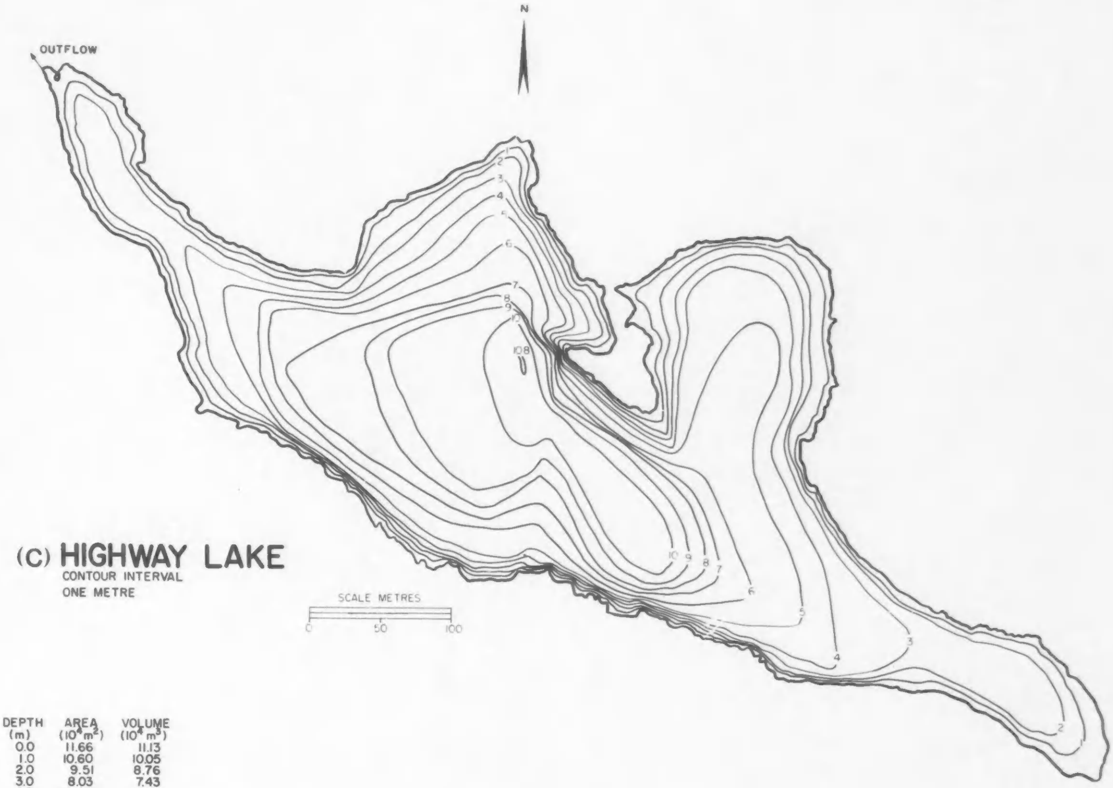
The lakes support a wide variety of invertebrates. Zooplankton communities are generally dominated by *Cyclops scutifer*, *Daphnia longiremis*, and *Diaptomus pribilofensis*, with each species most common in certain lakes. *Limnocalanus macrurus* has only been found in three lakes, all over 10 m deep. *Eubosmina longispina*, *Cyclops capillatus*, *Daphnia middendorffiana*, *Bosmina longirostris*, *Chydorus sphaericus*, and *Holopedium gibberam* are also present in some lakes. Abundance of planktonic crustacea varies from 2–10 individuals$\cdot L^{-1}$ in Methane Lake to 30–150 individuals$\cdot L^{-1}$ in Spring and Jade lakes. Zooplankton densities at Saqvaqjuac therefore range from typical Great Slave Lake values ($3\cdot L^{-1}$) to southern Lake Winnipeg values ($108\cdot L^{-1}$) (K. Patalas, Freshwater Institute, Winnipeg, Man., pers. comm.). The benthos has a large number of chironomids, as is typical of high arctic lakes (Welch 1976), and in addition, amphipods (*Gammarus l. lacustris*) and caddis flies (*Apatania zonella*, *Grensia praeterita*, and *Hesperophyllax* sp.) are abundant. Stoneflies and beetles are present but not abundant, except in lakes with no large fish, where beetles serve as top carnivores and become abundant.


OUTFLOW
N
(b) HAWK LAKE
CONTOUR INTERVAL
TWO METRES
SCALE METRES
0
50
100
INFLOW
20
18
16
14
12
10
8
6
4
2
34.4
34
32
30
28
26
24
22
20
18
16
14
12
10
8
6
20.4
7.4

DEPTH (m)	AREA ($10^4 m^2$)	VOLUME ($10^4 m^3$)
0	24.34	45.28
2	20.98	39.55
4	18.59	34.77
6	16.21	29.83
7.4	0.004	0.11
8	13.85	25.84
10	12.01	22.42
12	10.43	19.37
14	8.96	16.13
16	7.20	12.18
18	5.04	8.31
20	3.33	5.22
20.4	0.02	.09
22	2.19	4.01
24	1.83	3.20
26	1.38	2.53
28	1.15	2.07
30	0.93	1.51
32	0.60	.67
34	0.13	.01
34.2	0.03	

TOTAL VOLUME 2 834 370 m^3
MEAN DEPTH 11.65 m

FIG. 6. (*Continued*)



DEPTH (m)	AREA ($10^4 m^2$)	VOLUME ($10^4 m^3$)
0.0	11.66	11.13
1.0	10.60	10.05
2.0	9.51	8.76
3.0	8.03	7.43
4.0	6.85	6.12
5.0	5.42	4.63
6.0	3.89	3.49
7.0	3.02	2.62
8.0	2.23	1.94
9.0	1.66	1.11
10.0	.64	.19
10.8	.01	

TOTAL VOLUME = 591 689 m^3
MEAN DEPTH = 5.07 m

FIG. 6. (*Continued*)

TABLE 1. Morphometric features of Saqvaqjuac lakes.

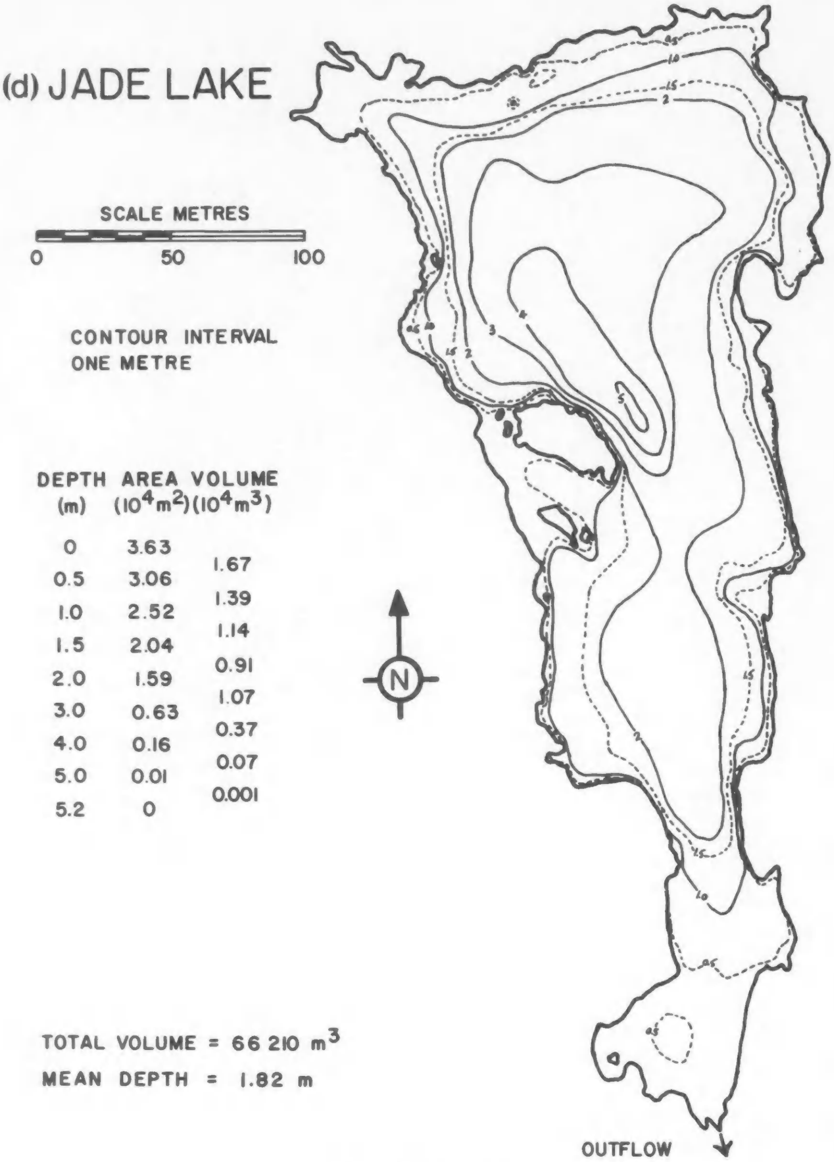
Lake	Z_{mean}	Z_{max}	$\bar{Z}:Z_{max}$	A_0 (ha)[a]	A_d (ha)[b]	$A_d:A_0$	% ice volume[c]	Elevation (m)[d]
Jade	1.82	5.2	0.35	3.63	27.9	7.7	77	31
Far	3.61	8.9	0.41	3.70	16.6	4.5	46	18
Hawk	11.65	34.2	0.34	24.34	299.4	12.3	16	4
Highway	5.07	10.8	0.47	11.66	38.9	3.3	36	2
Methane N.	4.29	11.3	0.38	5.24	19.35	2.2	38	19
Methane S.	5.98	15.3	0.39	3.41			29	
P&N	3.28	10.2	0.32	7.09	28.6	4.0	47	16
Spring	2.71	7.1	0.38	6.93	50.7	7.3	56	3
Turkey	10.78	29.4	0.37	41.25	3724.8	90.3	17	6
			$\bar{x}$ = 0.38					

[a] Lake area.

[b] Drainage area excluding lake area.

[c] Assumes 2 m ice thickness.

[d] P&N, Methane and Far from Dalton (1981), survey; Hawk from Cartographics Ltd. photogrammetric mapping; Jade, Turkey, Highway, and Spring from airphoto parallax measurements with an uncertainty of up to ±5 m (G. McCullough, Freshwater Institute, Winnipeg, Man., pers. comm.).

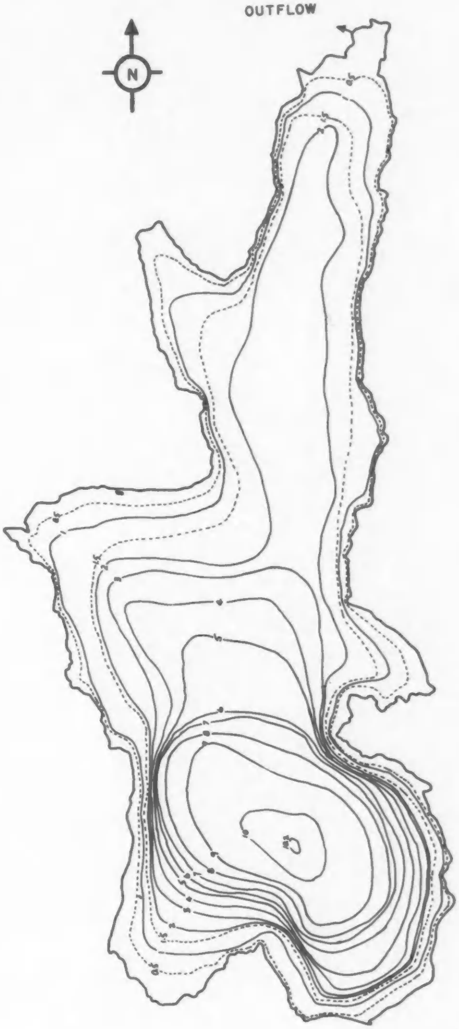

(d) JADE LAKE
SCALE METRES
0
50
100
CONTOUR INTERVAL ONE METRE
N
0.5
1.0
1.5
2
3
4
5
OUTFLOW

DEPTH (m)	AREA ($10^4 m^2$)	VOLUME ($10^4 m^3$)
0	3.63	
		1.67
0.5	3.06	
		1.39
1.0	2.52	
		1.14
1.5	2.04	
		0.91
2.0	1.59	
		1.07
3.0	0.63	
		0.37
4.0	0.16	
		0.07
5.0	0.01	
		0.001
5.2	0	

TOTAL VOLUME = 66 210 m^3

MEAN DEPTH = 1.82 m

FIG. 6. *(Continued)*


OUTFLOW
N
(e) P & N LAKE
CONTOUR INTERVAL
ONE METRE
SCALE METRES
0
50
100

DEPTH (m)	AREA ($10^4 m^2$)	VOLUME ($10^4 m^3$)
0	7.09	3.34
0.5	6.26	2.97
1.0	5.62	2.59
1.5	4.76	2.13
2.0	3.79	3.16
3.0	2.57	2.35
4.0	2.13	1.91
5.0	1.70	1.48
6.0	1.27	1.19
7.0	1.12	1.02
8.0	0.93	0.78
9.0	0.63	0.34
10.0	0.12	0.01
10.2	0	

TOTAL VOLUME = 232 700 m^3

MEAN DEPTH = 3.3 m

FIG. 6. *(Continued)*

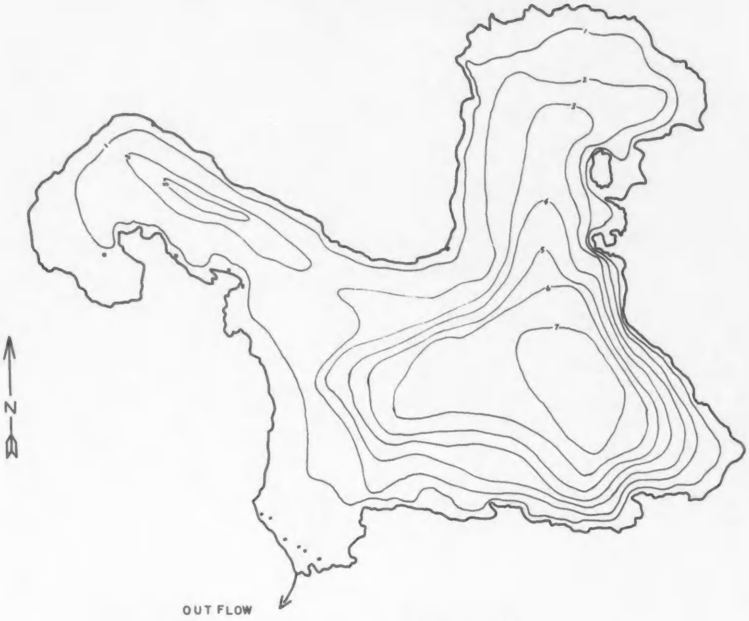
(f) SPRING LAKE

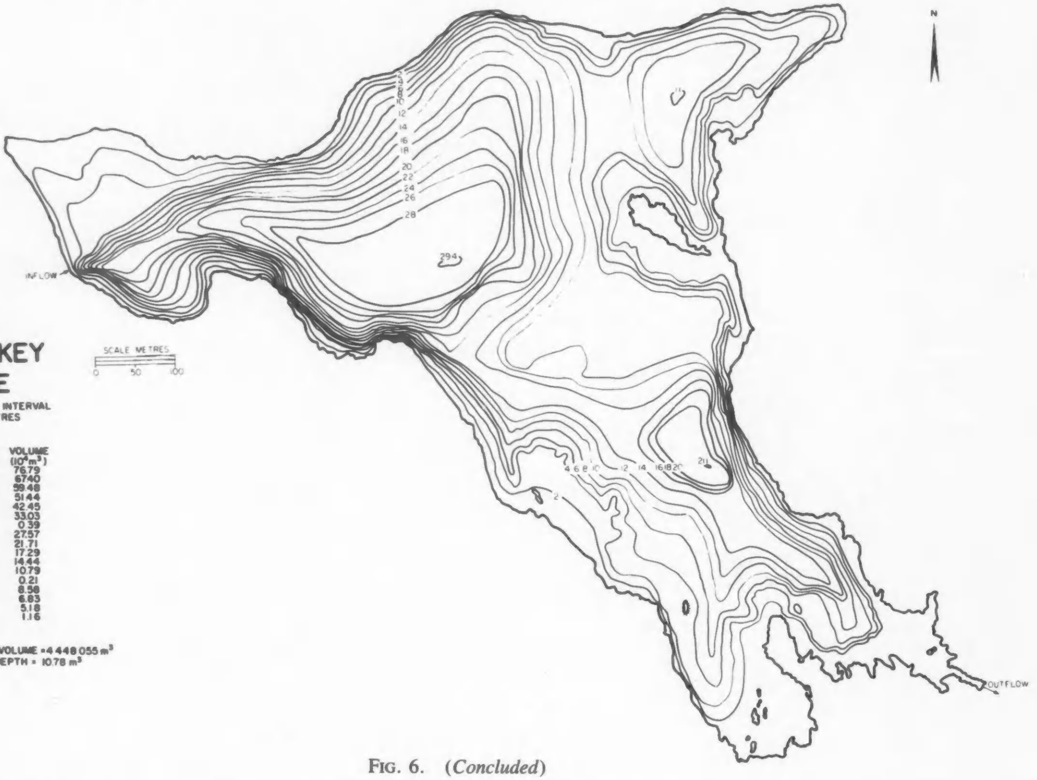
0 20 40 60 80 100 200
SCALE IN METRES

CONTOUR INTERVAL
ONE METRE

DEPTH (m)	AREA ($10^4 m^2$)	VOLUME ($10^4 m^3$)
0	6.94	6.07
1	5.25	4.31
2	3.44	2.89
3	2.37	2.05
4	1.74	1.53
5	1.33	1.13
6	0.95	0.60
7	0.32	0.11

TOTAL VOLUME 186 900 m^3
MEAN DEPTH 2.69 m





(g) TURKEY LAKE

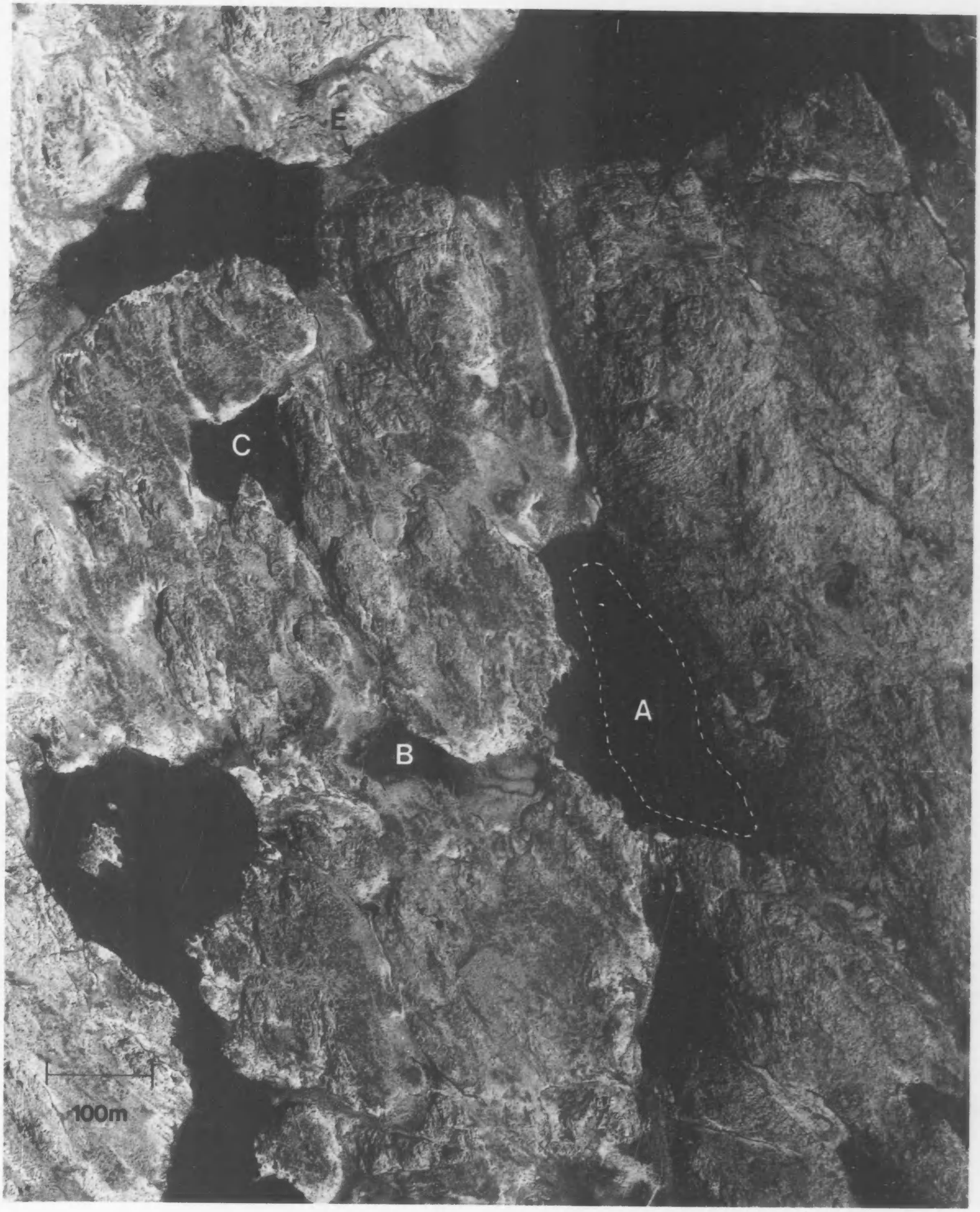
CONTOUR INTERVAL
TWO METRES

DEPTH (m)	AREA ($10^4 m^2$)	VOLUME ($10^4 m^3$)
0.0	41.25	76.79
2.0	35.61	67.40
4.0	31.82	59.48
6.0	27.71	51.44
8.0	23.78	42.45
10.0	18.77	33.03
11.0	0.02	0.39
12.0	15.23	27.57
14.0	12.39	21.71
16.0	9.39	17.29
18.0	7.93	14.44
20.0	6.54	10.79
21.1	0.01	0.21
22.0	4.76	8.58
24.0	3.84	6.83
26.0	3.05	5.18
28.0	2.15	1.16
29.4	0.04	

TOTAL VOLUME = 4 448 055 m^3
MEAN DEPTH = 10.78 m^3

FIG. 6. (*Concluded*)

FIG. 7. Aerial photograph of the Far Lake area. Saqvaqjuac lakes, here defined as water bodies >2 m deep that do not freeze to the bottom, are readily distinguished from ponds by the 2-m-deep shelf surrounding the lake margins. The 2-m contour is displayed for Far Lake (A). "Arts Pond" (C) is <1 m deep. Pond C is <2 m deep. These visual differences on aerial photographs are typical for lakes and ponds in this area of Keewatin. D = frost cracks in the till on the valley floor; E = willow cover. This aerial photograph, roll No. A31148-20, © August 24, 1976, Her Majesty the Queen in Right of Canada, reproduced from the collection of the National Air Photo Library with permission of Energy, Mines and Resources Canada.


E
C
D
A
B
100m

The fish fauna is impoverished on this part of the coast; several forms that are found south of Chesterfield Inlet and west toward Baker Lake are absent. Many (≈10%) of the lakes capable of supporting fish contain only nine spine sticklebacks (*Pungitius pungitius*), Methane and No-Fish lakes being good examples. Such lakes are invariably perched near the height of land and have outflows that are either too small or precipitous to allow fish to ascend, or else drain directly into the sea.[2] All other lakes have, in addition to stickleback, some combination of Arctic char (*Salvelinus alpinus*) and lake trout (*Salvelinus namaycush*). Although char and trout almost always appear together, a few of the smaller lakes may contain only one or the other, usually char, presumably either as a result of competitive exclusion or absence of colonization by the missing species. In large (>100 km^2) drainage systems there may be anadromous char present in addition to landlocked char and lake trout. In the Saqvaqjuac River the slimy sculpin (*Cottus cognatus*) is common, and threespine stickleback (*Gasterosteus aculeatus*) are also found; both probably occur nearby in larger drainages. Lastly, the burbot (*Lota lota*) is common to lakes of the larger drainages, including Saqvaqjuac River, Qaanigsluaajuq, Tuqaituq, and Turkey. The fourhorn sculpin (*Myoxocephalus quadricornis*) has not been taken in freshwater, although in the high arctic it is common in lakes that also hold anadromous char (H. E. Welch, pers. obs.).

Work carried out to date at Saqvaqjuac camp has been centered around a whole-lake phosphorus and nitrogen addition experiment, where phosphorus and nitrogen were added to P&N Lake and Jade Lake and phosphorus only to Far Lake, and Spring Lake served as control. It was hypothesized that added phosphorus and nitrogen would result in increased primary and secondary production quantitatively the same as found at ELA, and that this pulse of production would increase char and lake trout growth and biomass. Phosphorus addition alone was hypothesized to result in little if any immediate increase in primary production, but nitrogen fixation should increase. Detailed studies of meteorology, hydrology, chemistry, zooplankton, phytoplankton, primary production, physical limnology, benthos, and fish were made during this 7-yr experiment.

Another major study was a whole-lake addition of methane, which was hypothesized to increase oxygen consumption by methane-oxidizing bacteria. Although oxygen respiration did increase (Welch and Bergmann 1985), the effect was not enough to completely deplete the oxygen reserve of a lake in the event of accidental natural gas addition (Welch et al. 1980). A third study involved the dynamics of uranium series nuclides in aquatic food chains, partly because of the potential for commercial uranium extraction in the Baker Lake region 300 km to the west.

In summary, the area provides opportunity for whole-lake experiments, arctic estuarine work, and coastal Hudson Bay work from a comfortable, well-equipped facility.

Acknowledgments

I thank G. Brunskill, K. Patalas, and G. McCullough for providing information incorporated in this paper. R. Newbury, K. Beaty, G. McCullough, and A. Dalton surveyed the area and developed maps. The Saqvaqjuac meteorological site was established by A. Dalton and run by A. Dalton and C. Allan. The people of Chesterfield Inlet have been very helpful during the study, with special thanks to M. Kukkiak, G. Amarok, T. Amauyak, M. Kreelak, and J. Ipqarnaq. I extend my gratitude to the numerous summer students and support staff of the Freshwater Institute who made this work possible. John Loch and Gordon McRae were particularly instrumental in the Saqvaqjuac project.

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[2] As the land emerged from the Tyrrell Sea, fish were able to colonize new lakes. The actual fish biogeography of the area has not been worked out, however.

Water Circulation in Small Arctic Lakes in Winter

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Welch, H. E., and M. A. Bergmann. 1985. Water circulation in small arctic lakes in winter. Can. J. Fish. Aquat. Sci. 42: 506–520.

Dye experiments and detailed measurements of conductance and temperature in small lakes at Saqvaqjuac (63°39′N, 90°39′W), showed how water circulated in midwinter. Stored heat returning from the sediments warms adjacent water, which then sinks downslope. Water immediately beneath the ice moves laterally shoreward, picking up cryoconcentrated salts and sinking downslope. Displacement of deep waters upward at the lake center is postulated as completing the circulation. Rates of water movement are on the order of $10\,m \cdot d^{-1}$ in 2- to 10-ha lakes. This type of winter circulation is expected to be ubiquitous throughout the arctic.

La circulation de l'eau dans de petits lacs de Saqvaqjuac (163° 39′ N, 90° 39′ O) a été étudiée à l'aide de déversements de teinture et de quantifications détaillées de la conductance et de la température. La chaleur emmagasinée qui s'échappe des sédiments réchauffe les eaux avoisinantes qui s'enfoncent alors. Les eaux immédiatement sous la glace se déplacent latéralement vers le rivage en ramassant des sels cryoconcentrés, puis s'enfoncent. On formule l'hypothèse que le déplacement de masses d'eau vers le haut au centre du lac complète le cycle. Les taux de déplacement de l'eau s'élèvent à $10\,m \cdot jour^{-1}$ dans les lacs dont la superficie est de 2 à 10 ha. On s'attend à ce que ce genre de circulation hivernale soit omniprésent dans l'Arctique.

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It has been long assumed by limnologists that lakes must circulate beneath the ice. The bottom sediments gain heat from the water during summer and release it during winter. When unfrozen water is below 4°C, then warming of the water adjacent to the sediments should result in the sinking of water downslope (Birge et al. 1927; Hutchinson 1941; Stewart 1972; others). Such water movements have never been measured, to our knowledge, although their existence was clearly inferred from late winter distributions of temperature, oxygen, and other variables in Tornetrask (68°N, Sweden) (Mortimer and Mackereth 1958). Likens and co-workers (Likens and Hasler 1962; Likens and Ragotzkie 1965) traced water movements beneath the ice of Tub Lake (Wisconsin) using radiosodium as a tracer. Much of the unfrozen lake was *above* 4°C and heating by the bottom resulted in upward water movement, to be met by downward movement caused by cooling at the ice surface; the resulting circulation pattern was therefore complex and fundamentally different from that of a lake whose water is less than 4°C.

In small arctic lakes, typical isopleths of conductance and temperature (Fig. 1 and 2) suggest that the lakes are stratified and stable, with little or no vertical water movement during the midwinter period (November–April). However, we have suspected that there must be considerable vertical movement, if not complete circulation, based on the following evidence:

(1) There is no net change in the mass of conservative elements beneath the ice over winter (Schindler et al. 1974; H. E. Welch and J. Legault, in prep.). Concentration changes are due to freezeout or cryoconcentration, the exclusion of dissolved substances from water as it freezes. If the excluded salts did not move vertically, there could be concentration changes only in the water immediately below the subice surface, but this is not the case because salts also concentrate in the bottom water, as well as increasing in the center of the water column (Fig. 1).

(2) One of us (H.W.), while diving in Char Lake (Resolute Bay, N.W.T.) in late winter, observed that anaerobic water collected in depressions in the moss cover between 3 and 15 m depth and that this anaerobic water apparently ran slowly downslope from one depression to the next, as evidenced by moss blackened by the anaerobic water. It was thought at the time that this constituted part of an overall lake circulation during winter.

(3) Areal oxygen consumption by bottom sediments between 15 and 27 m in Char Lake is constant and depth-independent (Welch and Kalff 1974). Since practically all winter respiration in Char Lake occurs on the bottom, winter oxygen comsumption by each metre horizontal stratum should, therefore, be a constant function of the sediment area exposed at each stratum. However, a plot of respiration versus exposed surface area has much scatter, and the rates are about half of the actual bottom water–sediment respiration rates (data not shown). Therefore, there must be a net transfer of oxygen from shallow depths into the 15–27 m zone by water currents, since molecular diffusion alone could not account for the quantities and distance moved.

From the preceding evidence we concluded that polar lakes circulate during the winter. Assuming that currents residual from before freezeup are negligible, there are two possible

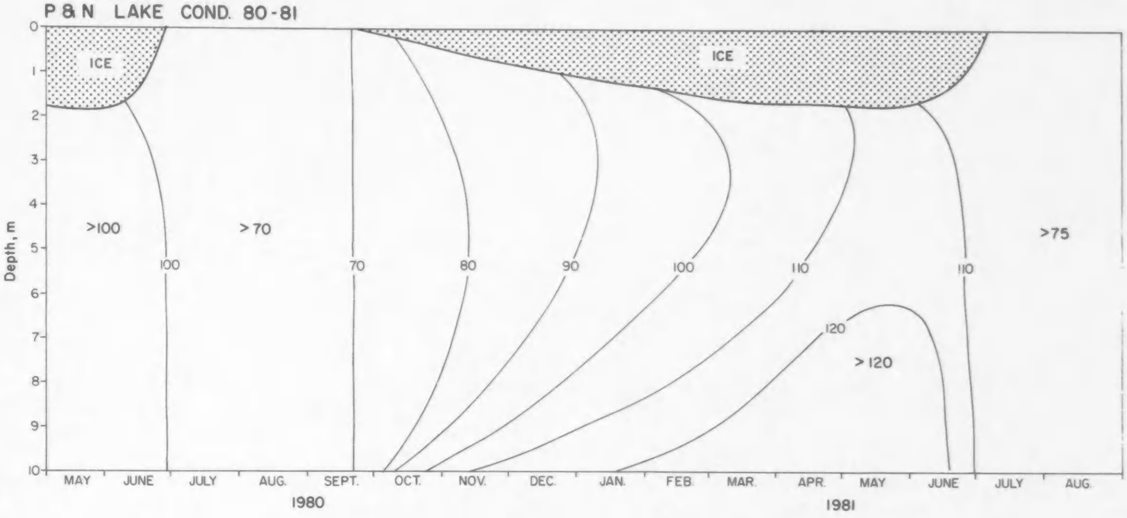

FIG. 1. Isopleths of conductance ($\mu S \cdot cm^{-1}$) in P&N Lake, 1980–81.

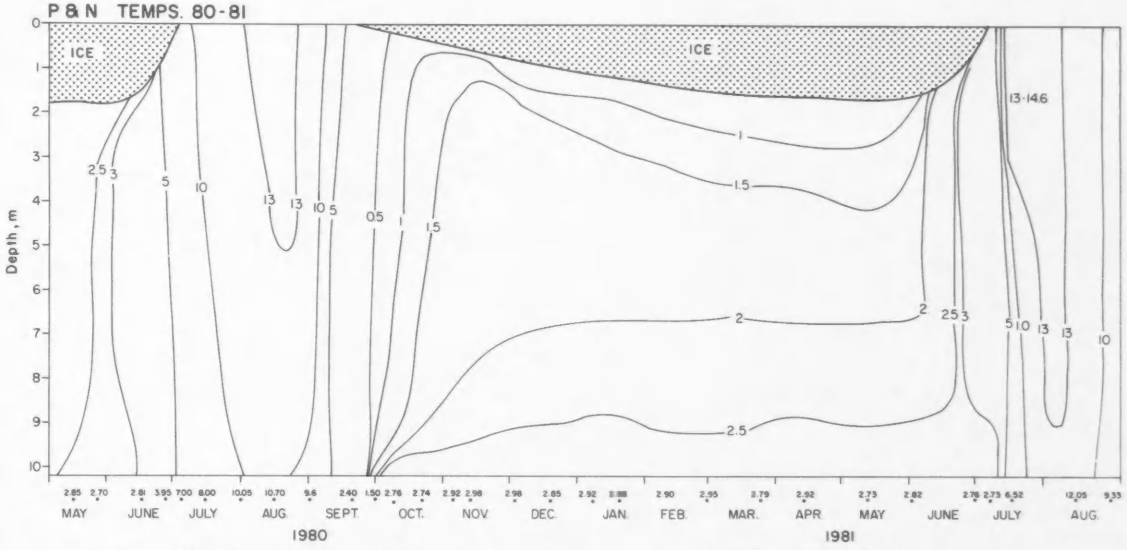

FIG. 2. Isotherms in P&N Lake, 1980–81. Numbers below the graph are degrees Celsius 2 cm into the bottom sediment.

driving forces for such circulation: freezeout and heat. Freezeout results in concentration of dissolved substances which increase the water density and might cause vertical density currents, as suggested by Schindler et al. (1974) for Char Lake. Heat sources include solar radiation, the oxidation of organic matter (a negligible amount), geothermal heat flow, and the return of stored summer heat from the lake bottom. In this paper we will discuss only the midwinter period (November–May) when radiative heating is negligible. Geothermal heat flow we assume is zero, since the area is underlain by >300 m of permafrost (Brown 1977) and the lakes under discussion are small (<20 ha). This leaves the return of stored heat from the bottom as a heat source.

Since arctic lakes always freeze after the lake body has cooled below the temperature of maximum density, and frequently to within a few tenths of 0°C, any subsequent heat transfer from the bottom to the overlying water column will cause a downslope density current. We also expect there must be lateral shoreward currents beneath the ice which replace water sinking downslope. Water made denser by freezeout will also sink and be transported laterally, shoreward, there to sink and run downslope along the bottom, contributing to overall circulation (Fig. 3). To complete the circulation there may be upwelling at the lake center although we do not know how this would work (see also Discussion).

We tested this hypothesis at Saqvaqjuac, a Department of Fisheries and Oceans Canada research camp on the northwest coast of Hudson Bay (63°39′N, 90°39′W), where numerous

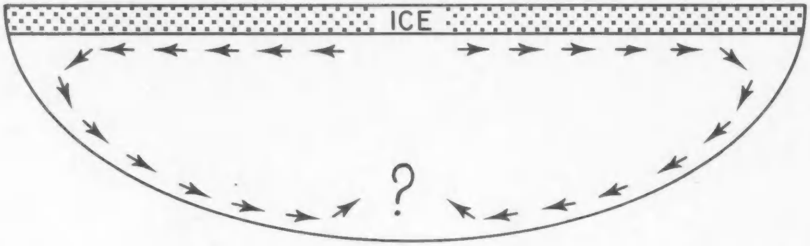

FIG. 3. Proposed model of midwinter lake circulation.

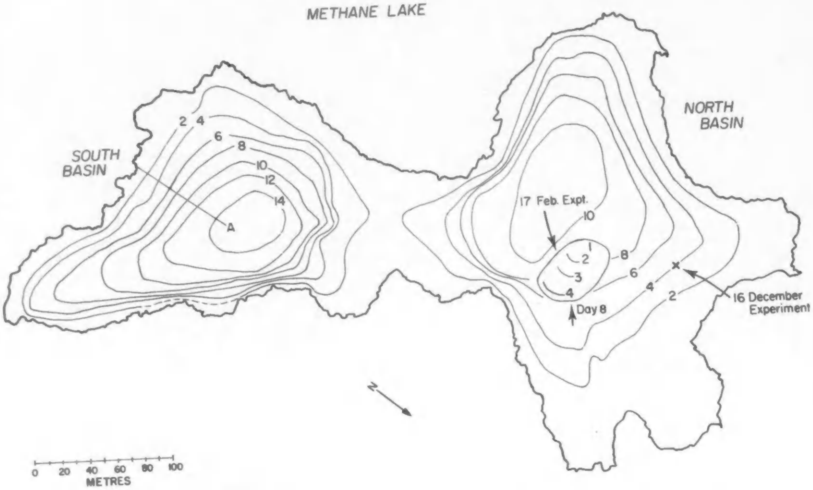
METHANE LAKE
SOUTH BASIN
NORTH BASIN
2
4
6
8
10
12
14
A
17 Feb. Expt.
10
1
2
3
4
8
6
4
2
Day 8
16 December Experiment
N
0
20
40
60
80
100
METRES

FIG. 4. Morphometry of Methane Lake, showing horizontal dye movements.

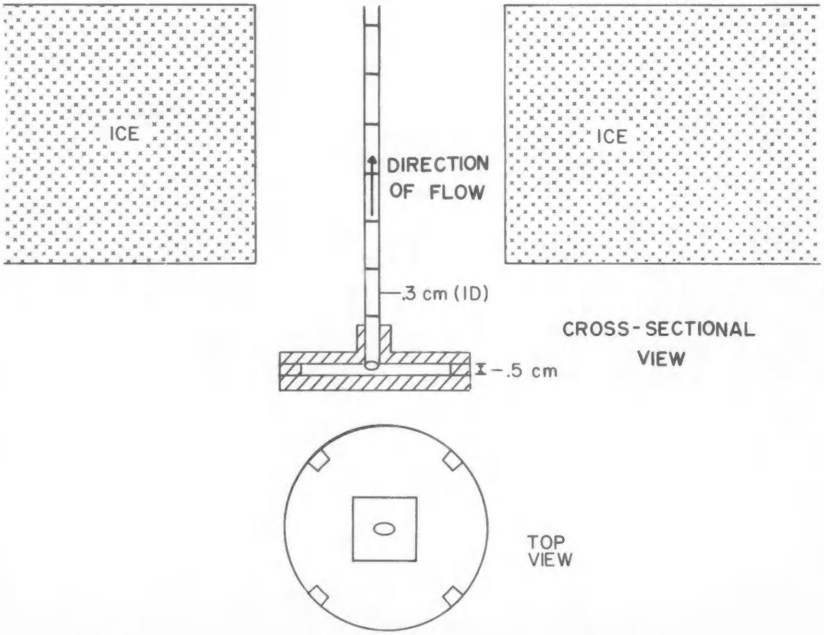
ICE
DIRECTION OF FLOW
ICE
.3 cm (ID)
CROSS-SECTIONAL VIEW
.5 cm
TOP VIEW

FIG. 5. Tube and baffle used to add dye, and to take stratified water samples.

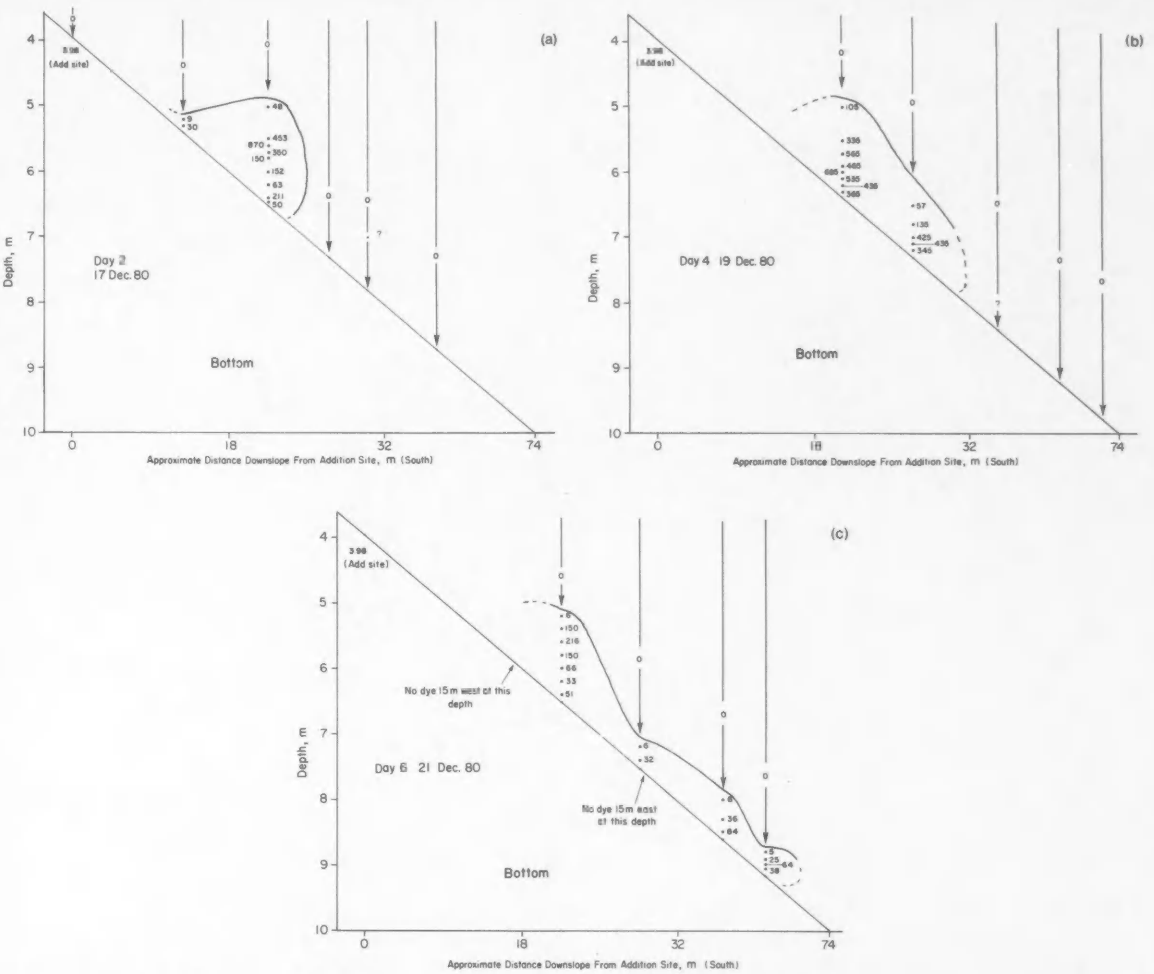

FIG. 6. Dye profiles in Methane North after addition at 3.98 m, showing approximate limits of detectability. Numbers are relative fluorometric concentrations.

small lakes on Precambrian Shield bedrock provide experimental systems (see Welch 1985). Detailed profiles of conductance and temperature were made to determine whether density patterns were consistent with the hypothesis. Additions of rhodamine dye were also used to follow water movements beneath the ice.

Methods

Lakes selected for study were Methane North, Methane South, and Lower No-Fish. Detailed morphometry is known only for Methane Lake (Fig. 4). Lower No-Fish is 8.8 ha and has a maximum depth of 13 m.

Temperature measurements were made with a 2-mm-diameter thermistor bead extending 2 cm below an 8-cm-diameter weighted baffle. The cable was marked in 1-cm intervals to allow precise determination of the thermistor depth relative to the lake bottom. A digital-readout ohmmeter coupled to the thermistor gave a resolution of 0.03°. The unit was calibrated against a slush bath (0°C) and a high-precision mercury thermometer (0.1° divisions).

Conductance samples were taken by sucking samples from each depth through a horizontal baffle (Fig. 5) to sample layers no thicker than ≃1 cm at each depth. Particular care was taken to ensure that water from the previously sampled depth was flushed from the apparatus. Precision was ±0.5%, about equal to $\pm 0.03\ \mu S \cdot cm^{-1}$.

Dye additions utilized 100–750 mL of concentrated (30% by mass in glacial acetic acid) rhodamine B solution diluted 25:1, cooled to 0°C, and siphoned into each lake through a 10-cm-diameter horizontal baffle (Fig. 5) at a rate $<1\ L \cdot min^{-1}$ at the desired depth. Observations of horizontal and vertical dye distribution were made using the same sucker sampler used for conductance. Relative dye concentrations were determined by fluorometry using a Turner model III with flow-through door, and by noting the color strength of the water in an in-line 125-mL Erlenmeyer flask as it flowed from the sample hose to the fluorometer.

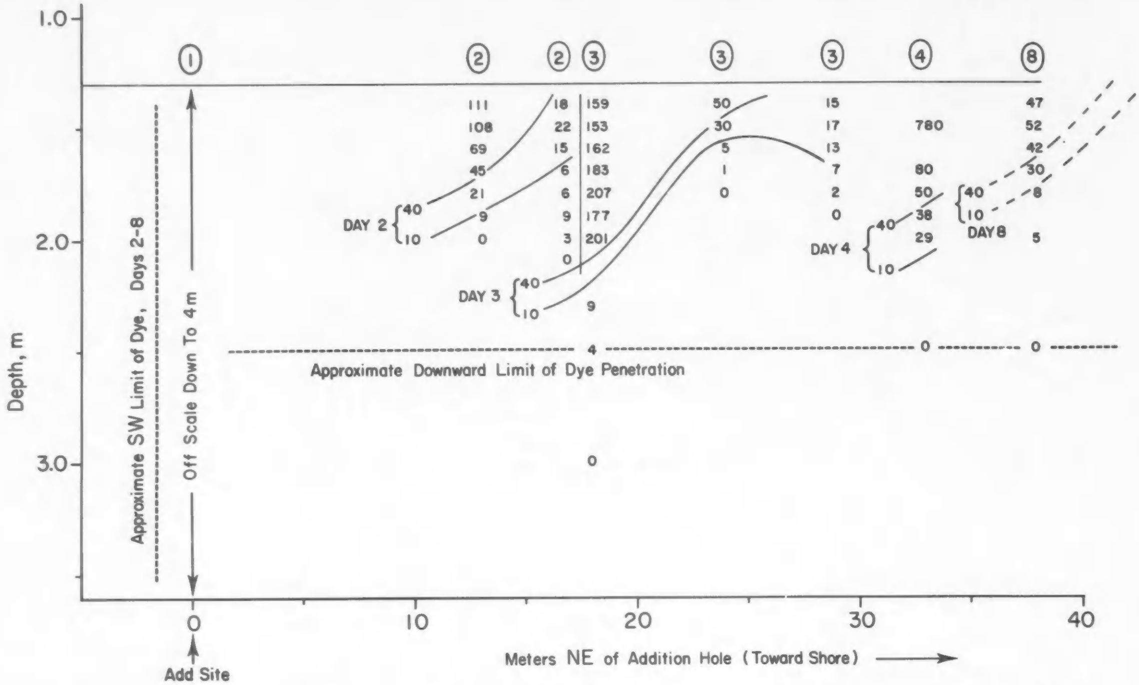

FIG. 7. Dye profiles in Methane North following a subice addition on 17 February 1981 (day 1). Circled numbers define profiles by day of the experiment. Isopleths of relative dye concentration by day are shown.

Results

Methane North Dye Addition to Bottom Water

On 16 December 1980, 100 mL of 30% rhodamine was added at 3.88 m in 3.98 m of water below 0.98 m of ice (Fig. 4). We were able to follow the dye for 6 d as it progressed directly toward the center of the lake (Fig. 6a–6c), but by day 9 we could no longer locate it. We were unable to detect the dye laterally more than a few metres on either side of a line between the addition site and the center of the lake, nor was the dye found shallower than the addition site. Note in Fig. 6 that the water closest to the bottom often had lower concentrations of dye than water a metre or so above the bottom.

The results of this experiment are consistent with the hypothesis whereby water adjacent to the bottom is warmed and sinks toward the center of the lake.

Methane North Dye Addition to Subice Water

On 17 February 1981, 600 mL of 30% rhodamine was added at the ice–water interface over 9 m of water (Fig. 4). Ice thickness averaged 1.3 m. Six hours after addition, dye was detectable to a depth of 4.5 m but nearly all of it remained in the top 1.5 m of water where it had been injected. Over the next 7 d the dye was detectable only in the topmost metre of water and was most concentrated 10–20 cm below the bottom ice surface (Fig. 7). It moved gradually toward shore (see Fig. 4) and we ceased observations after day 8. These results are consistent with the circulation model.

Upper No-Fish Dye Addition

On 19 March 1981 we added 750 mL of 30% rhodamine at the ice–water interface over 5.8 m of water. Because of time constraints we did not make more than a few fluorometric readings, but rather described the color of the water as it passed through an Erlenmeyer flask in the suction train. (These brief descriptions (very pink, pink, faint pink, very faint pink, barely detectable) were translated into the stipple marks on Fig. 9a–9d.) The dye progressed generally shoreward into shallower water (Fig. 8), although the plan view is misleading because it includes all depths. At first it was found at or near the bottom ice surface (Fig. 9a) but as it moved shoreward it sank (Fig. 9b) so that by day 7 dye could be found throughout the water column but was most concentrated near the bottom and, in shallow water, near the lower ice surface (Fig. 9c). By day 12 (Fig. 9d) the dye was mostly detectable in bottom water deeper (further from shore) than the addition site. These results are again consistent with the conceptual model. Interestingly, we did not find dye in water less than 3 m deep. It appeared to sink in the 3–5 m zone.

Observations of Temperature and Conductance

Detailed temperature measurements from the north and south basins of Methane Lake in early December 1980, and for Upper No-Fish later in the winter, show that isotherms were not all horizontal, but tended to bend downwards near the lake edges (Fig. 10–12). Both Methane North and Upper No-Fish data clearly showed temperature inversions near the bottom, whereby

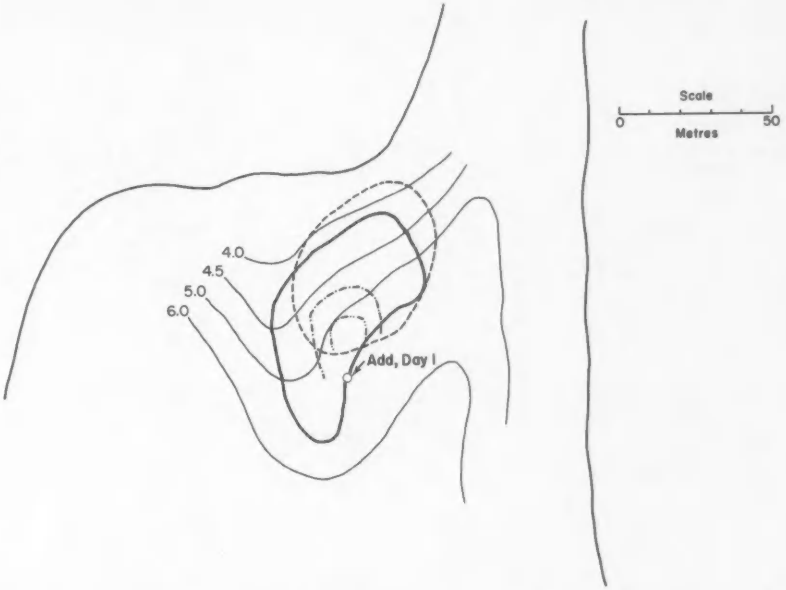

FIG. 8. Horizontal dye movements in Upper No-Fish. Plan view showing outermost limits of dye distribution. -···-, day 3; -·-, day 5; —, day 7; ---, day 9.

a wedge of slightly warmer water lay between the bottom few centimetres and a metre or so above that (Fig. 10 and 12). In all Saqvaqjuac lakes, bottom sediment temperatures are higher than in the overlying water, although shallow rocky bottoms may not show this (e.g. Fig. 12, stations 2 and 3).

Conductance at the deepest station was lower near the middle of the water column (Fig. 13 and 14), as expected from seasonal isopleths (Fig. 1). But again, these isopleths are not horizontal, but rather dip under as the side of the lake is approached. At a given depth, salt concentrations were lowest in the center of the lake and increased shoreward.

Using an empirically derived relationship for Saqvaqjuac lakes (unpubl.) where

$$(1)\quad [\text{Total dissolved solids (TDS) } (\text{mg}\cdot\text{L}^{-1}) = 0.2751\ (\mu\text{S}) + 3.6836]$$

and water density as a function of temperature as given by Kell (1975), we calculated water densities for the data points from Methane North (Fig. 15). There appear to be small anomalies at some stations, suggesting that the water adjacent to the bottom is not stable. The density isopleths in Fig. 15 follow temperature more closely than conductance (see Discussion). Densities for Methane South could not be calculated because temperature and conductance were measured on different days.

These data are consistent with the hypothesis that water adjacent to the bottom picks up heat from the sediments, becomes denser, and hence sinks downward and slowly progresses downslope as it continues to warm. It is replaced by water beneath the ice moving slowly outward from the center to the sides, picking up cryoconcentrated salts and increasing slightly in conductance as it does so. In turn, it warms and sinks when it reaches the shore.

Discussion

We conclude that water in the three lakes studied does in fact circulate according to the conceptual model presented in Fig. 3. We have found similar winter temperature and conductive structure for all lakes tested in the Saqvaqjuac area, including lakes to 34 m deep. Lakes in the high arctic also have similar heat and dissolved solids profiles during winter (Schindler et al. 1974; H. E. Welch, unpubl.). We expect, therefore, that virtually all small and medium-sized arctic lakes circulate in like manner during winter.

Mortimer and Mackereth (1958), working with late winter profiles of oxygen, temperature, conductance, and alkalinity from subarctic Lake Tornetrask, concluded that the limnological differences between basins must have resulted from the downslope sinking of water due to the release of stored summer heat from the bottom. Our dye experiments confirm that proposed circulation. Although we do not have data on undisturbed multiple basin arctic lakes (but see Welch et al. 1980), we expect that such lakes will develope interbasin differences in limnological parameters as a consequence of vertical circulation, even though the lakes enter freezeup in a homogeneous state.

Although we had no means of measuring the density of the dye solution used in the tracer experiments, circumstantial evidence indicates that there was no signifcant difference in density between the dilute, cold solution and the surrounding water. The Methane North subice addition remained immediately below the ice and did not sink; the Methane North bottom water addition moved downslope and did not float; and the No-Fish subice addition did not sink immediately but rather moved shoreward beneath the ice, then sinking and moving

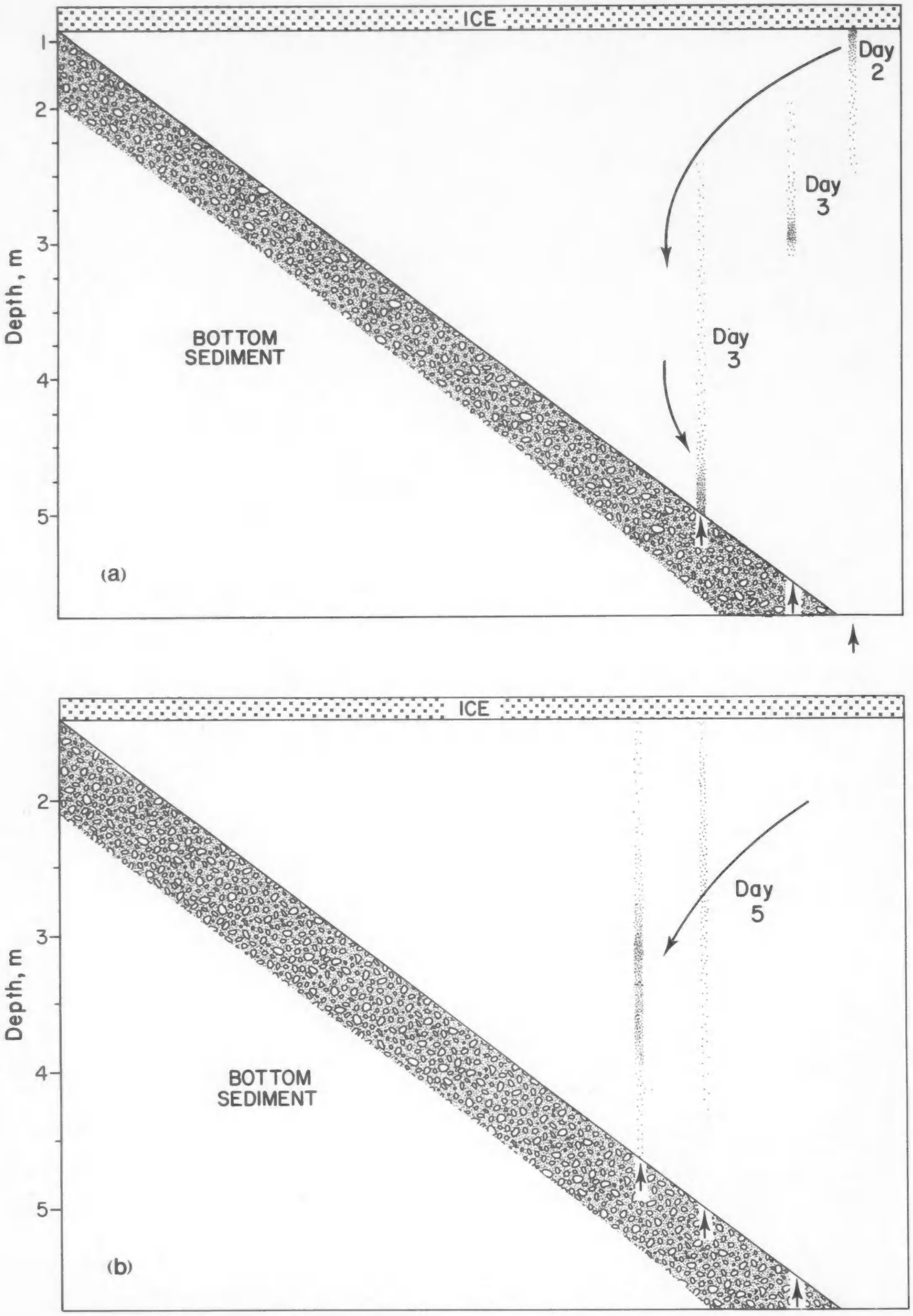
ICE
Day 2
Day 3
Day 3
BOTTOM SEDIMENT
Depth, m
1
2
3
4
5
(a)
ICE
Day 5
BOTTOM SEDIMENT
Depth, m
2
3
4
5
(b)

FIG. 9. Dye distribution in Upper No-Fish on (a) days 2 and 3, (b) day 5, (c) day 7, and (d) day 12.

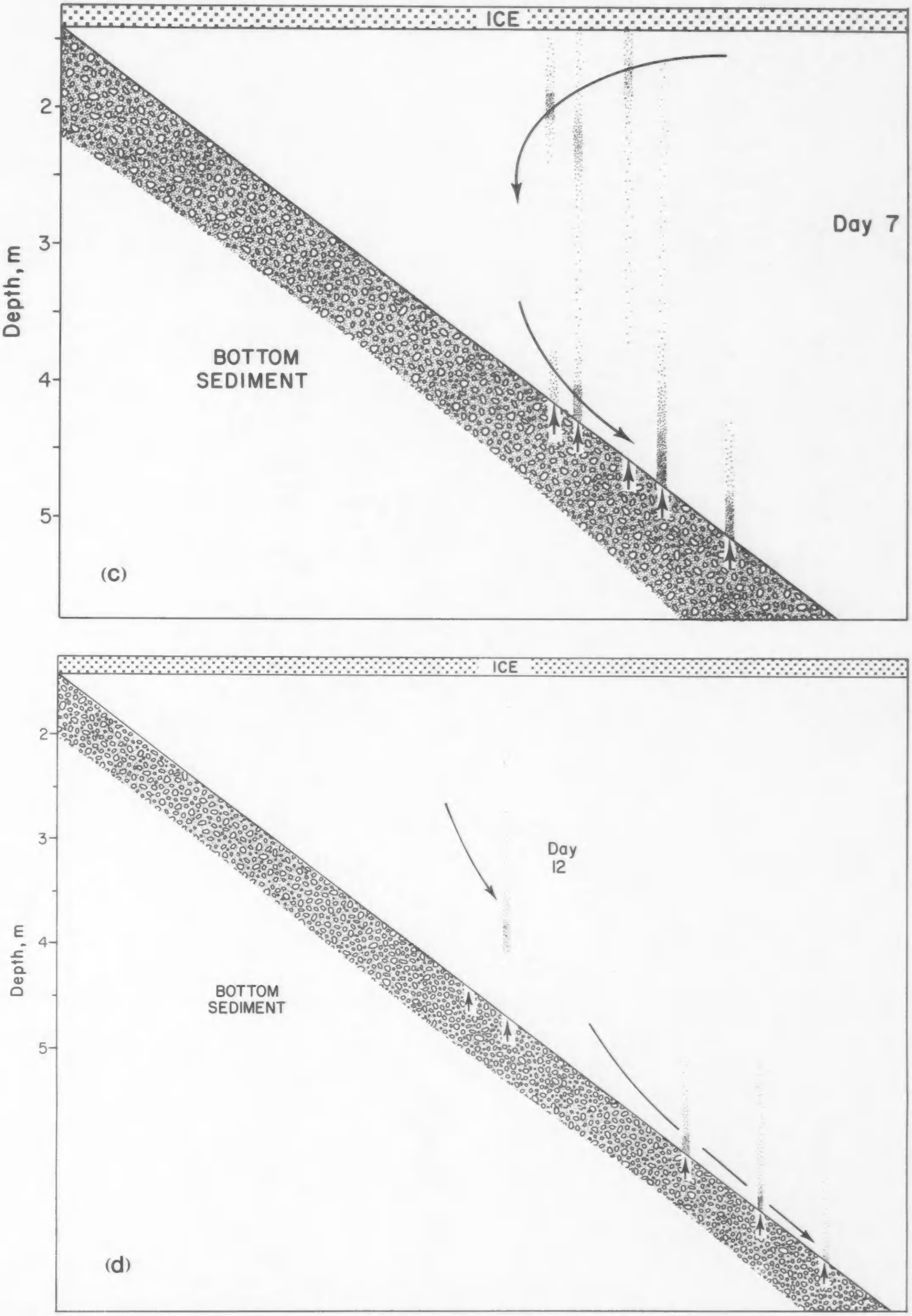
ICE
2
3
4
5
Depth, m
Day 7
BOTTOM SEDIMENT
(c)
ICE
2
3
4
5
Depth, m
Day 12
BOTTOM SEDIMENT
(d)

FIG. 9. (*Concluded*)

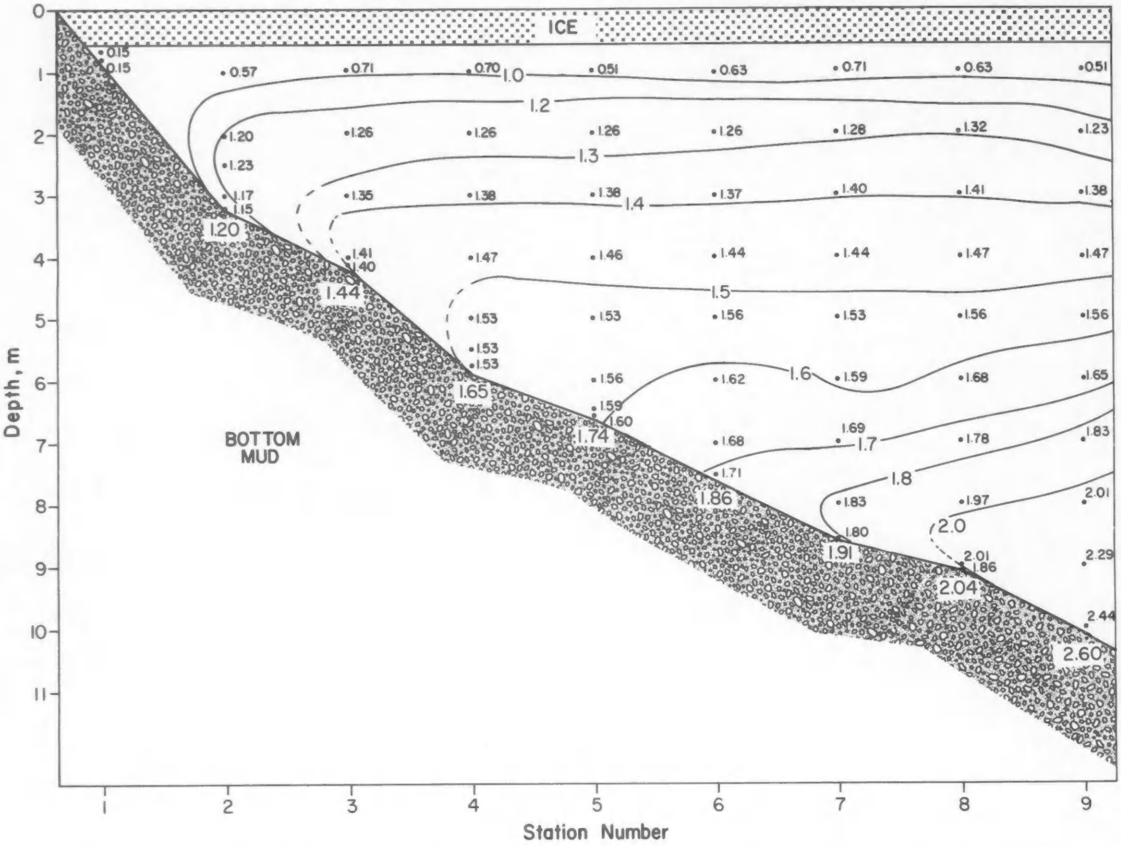

FIG. 10. Isotherms in Methane North, 3 December 1980. Numbers in the shaded area are temperatures 2 cm into the bottom mud.

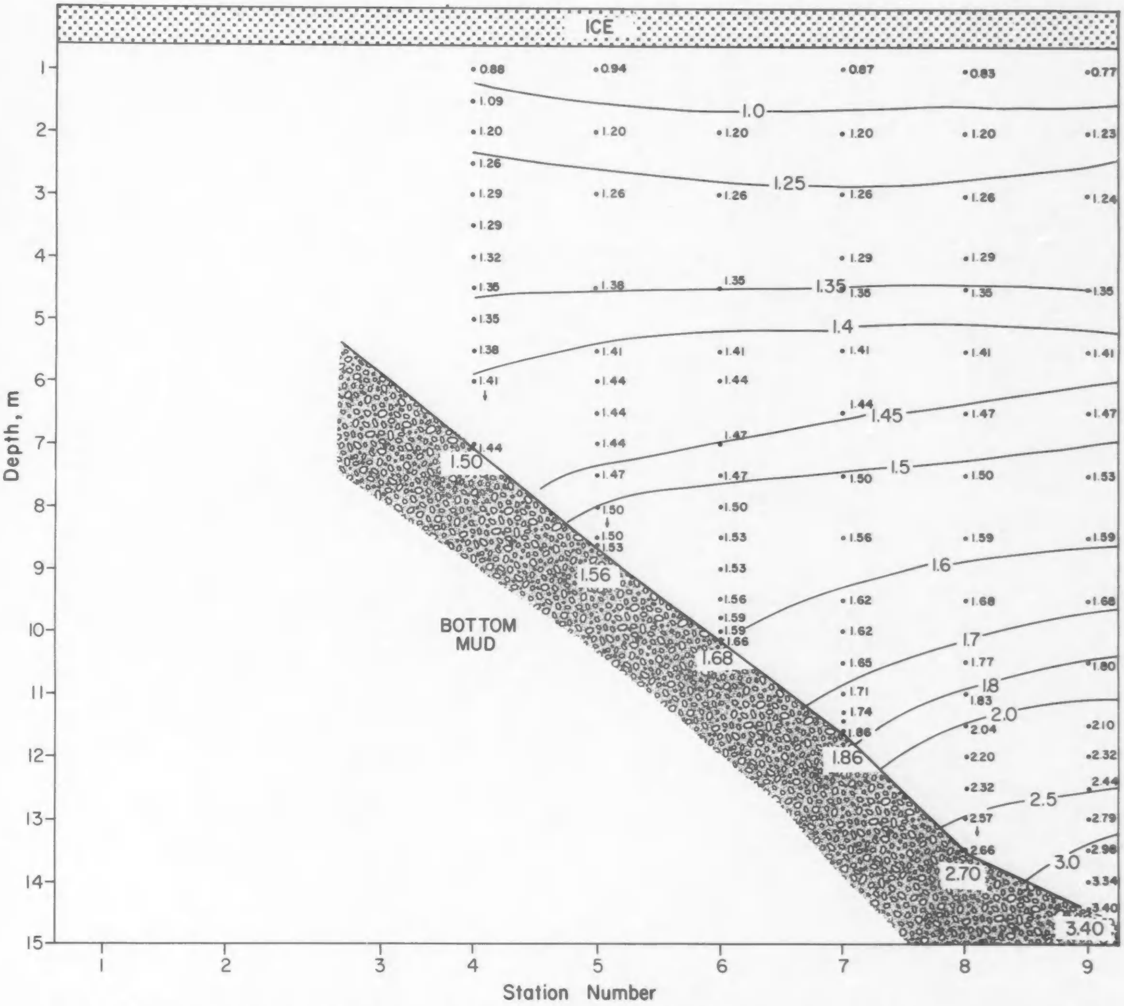

FIG. 11. Isotherms in Methane South, 28 November 1980. Numbers in the shaded area are temperatures 2 cm into the bottom mud.

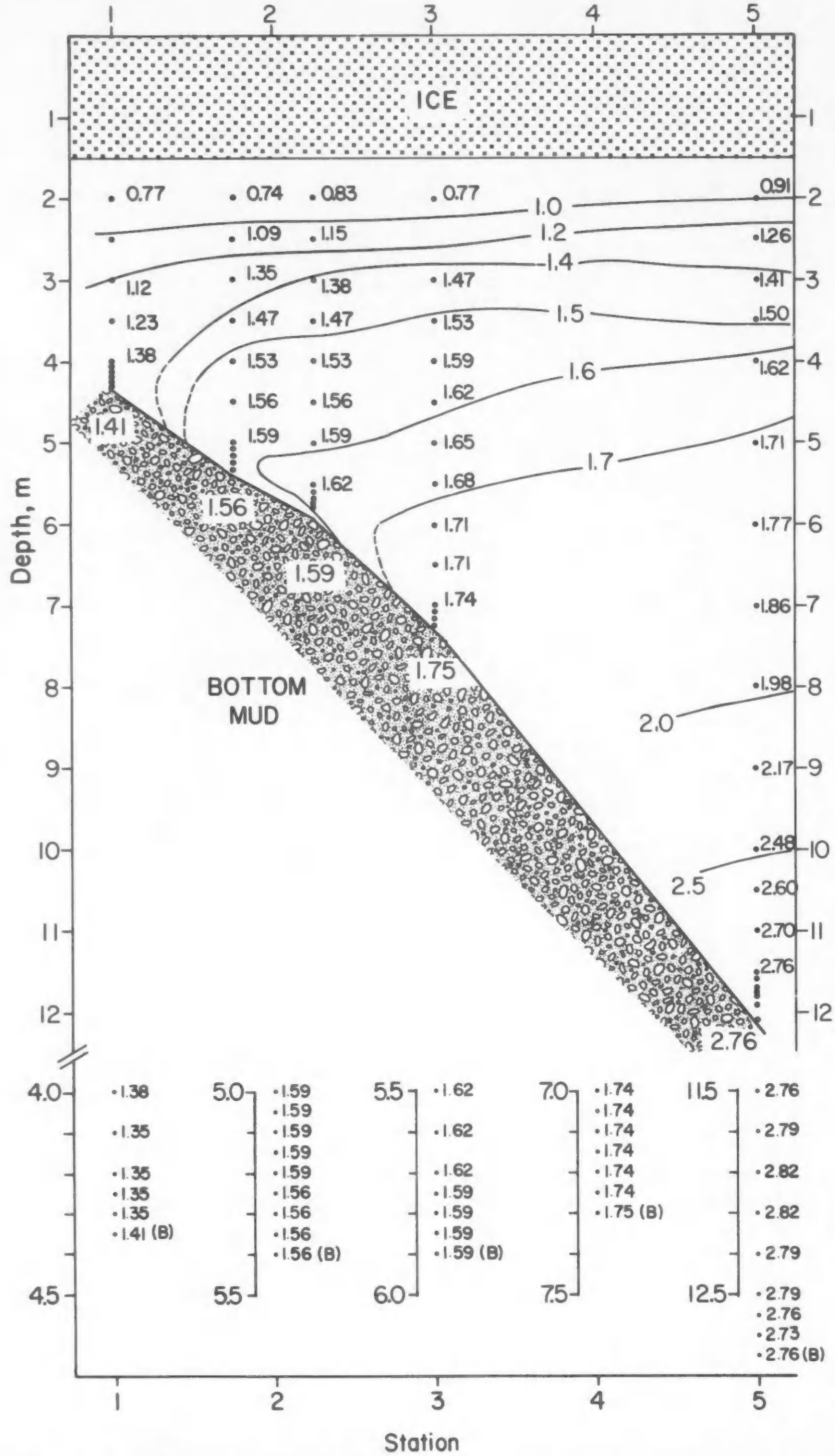

FIG. 12. Isotherms in Upper No-Fish, 23 March 1981. Numbers in the shaded area are temperatures 2 cm into the bottom mud. Detailed temperatures are shown for bottom water at each station.

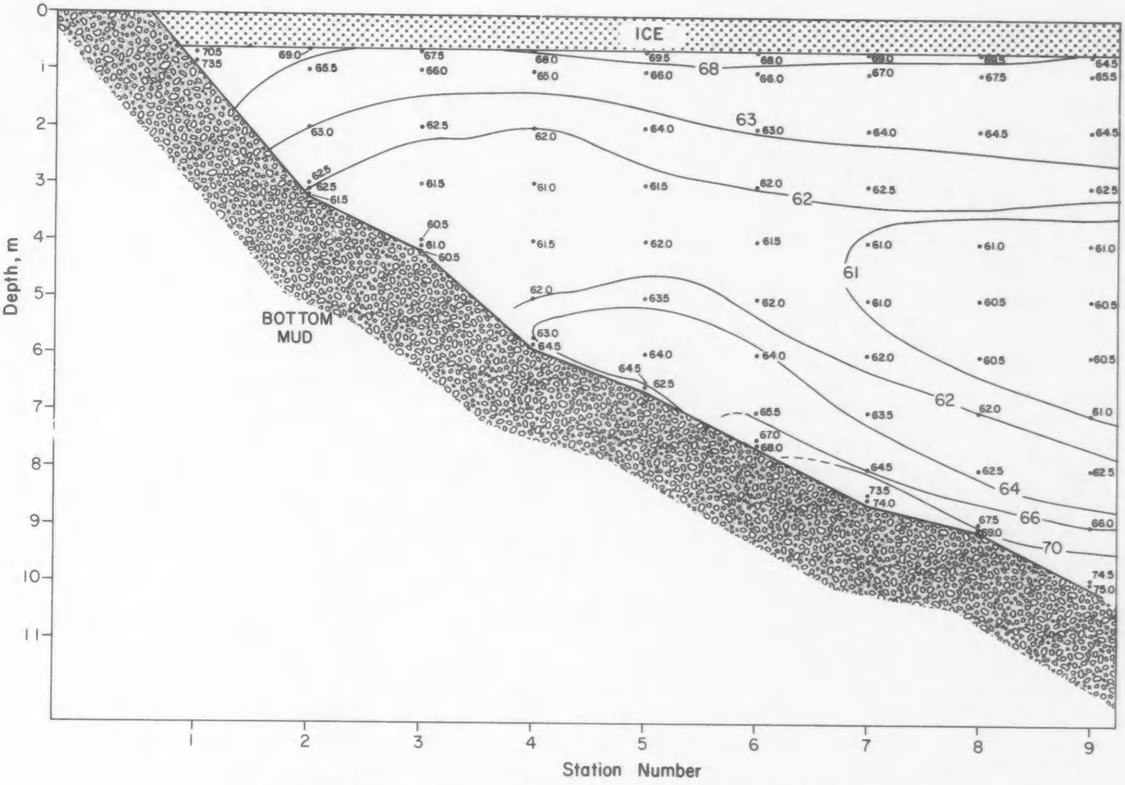

FIG. 13. Isopleths of conductance, (μS·cm^{-1}) in Methane North, 3 December 1980.

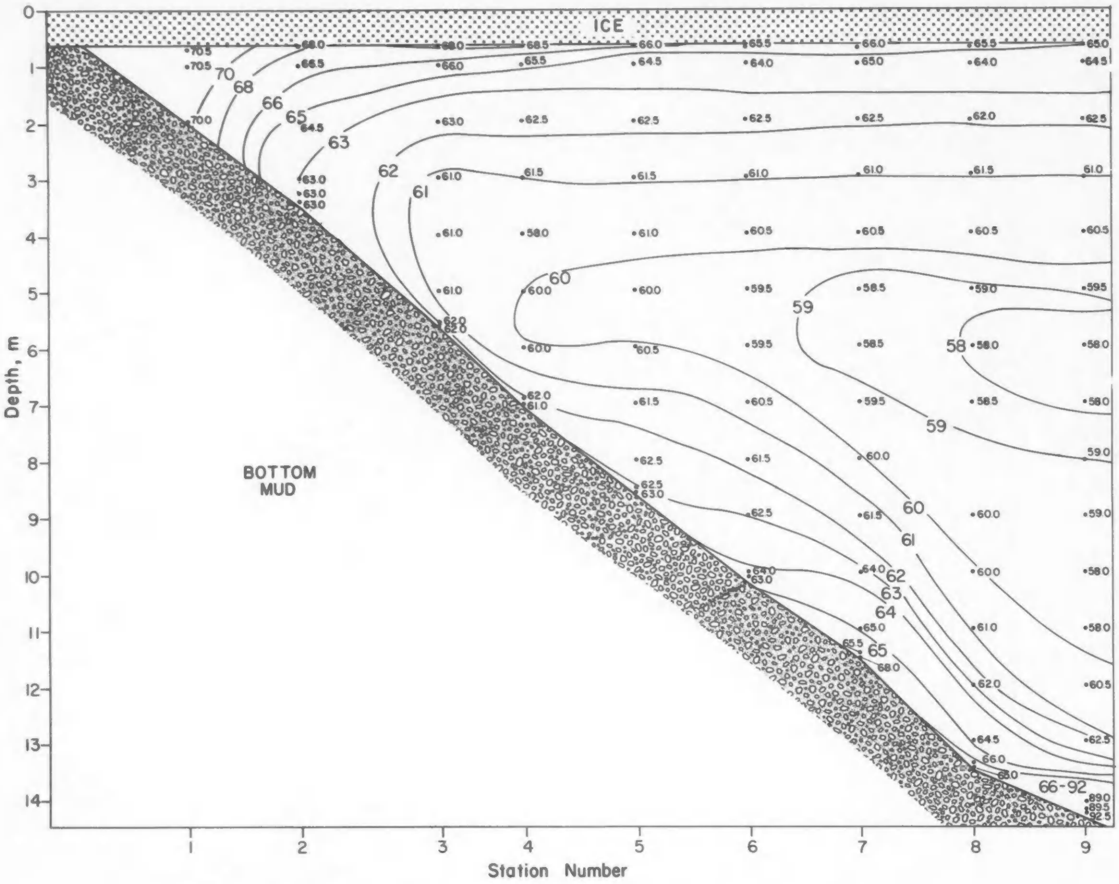

FIG. 14. Isopleths of conductance, ($\mu S \cdot cm^{-1}$) in Methane South, 1–2 December 1980.

downslope according to the proposed circulation scheme. We therefore conclude that the dye movements were not caused by significant differences in density between the tracer and the surrounding water.

Rate of Water Movement

In the Methane North subice experiment, the leading edge of the dye moved shoreward at an apparently decreasing rate, although dilution of the dye and resultant lower detectability at the leading edge probably contributed to this apparent decrease (Fig. 7). In that experiment, the trailing edge of the dye mass remained approximately at the addition site, whereas the leading edge progressed shoreward about $10\,m \cdot d^{-1}$. Assuming the dye mass expanded outward evenly in all directions due to random spreading effects (diffusion, turbulent transport, residual momentum from the addition), the expansion was therefore $10\,m \cdot d^{-1}$ and the overall rate of water movement $5\,m \cdot d^{-1}$, and probably more.

In the Methane North bottom water experiment (Fig. 6), the dye progressed toward deep water at about $10\,m \cdot d^{-1}$, but random spreading effects were much less than half this rate because on day 2 no dye was detectable at the addition hole and very little about 15 m downslope from there, and on day 6 no dye was detectable 15 m on either side of the main mass of dye as it moved downslope. Net rates of water movement, therefore, were most likely between 5 and $10\,m \cdot d^{-1}$ beneath the ice, and closer to $10\,m \cdot d^{-1}$ near the lake bottom.

In the deep water experiment, we also found suggestions of very narrow bands of dye in advance of the leading edge (Fig. 6); as we slowly raised and lowered the baffle and sucker sampler, brief blips occasionally showed up on the fluorometer but attempts to stop and locate these layers always failed. If they were real, they suggest that density currents may form, progress downslope, and run out horizontally in thin layers as they reach water of equal density. The isopleths of temperature (Fig. 10 and 11) and density (Fig. 15) certainly imply a dynamic and somewhat instable system with continual movement.

At water movement speeds on the order of $10\,m \cdot d^{-1}$ in 5- to 20-ha lakes, water will have moved from beneath the ice at lake center to the shore, or from shore to maximum depth on the bottom in 10–14 d.

Driving Forces

Heat

The mean temperature difference between the bottom sediments and the overlying water is 0.12° in Methane North, 0.03° in Methane South, and 0.02° in No-Fish (Fig. 14–16). If we therefore assume an approximate thermal gradient near the

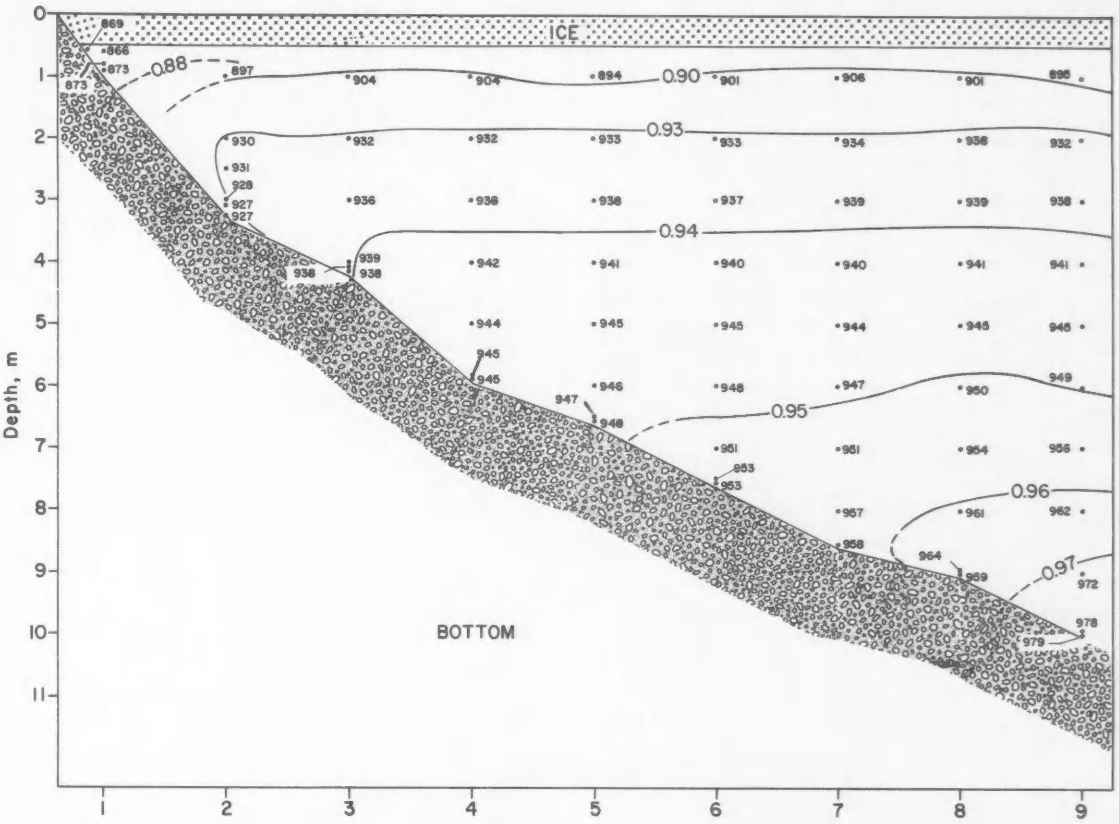

FIG. 15. Isopleths of calculated density in Methane North. All numbers are the fourth to seventh decimal place and are actually preceded by 0.999----.

bottom of 0.03°·cm^{-1}, and use a thermal molecular diffusivity of 1.2×10^{-3}·cm^{-2}·s^{-1} (Hutchinson 1957), we find a flux of about 13.0 J·cm^{-2}·d^{-1}, or 2720 J·cm^{-2} for the midwinter period (November–May). This heat input is balanced by heat loss through the ice, where the thermal gradient in the half metre of water directly below the ice ranges from ≃0.05°·cm^{-1} in October to 0.015°·cm^{-1} in March (H. E. Welch and J. Legault, unpubl.), resulting in no net change in mean water temperature during the midwinter period (Fig. 2). Were this heat flux to remain in water adjacent to the bottom, the rise in water temperature would be rapid and obvious; e.g. a flux of 13 J·cm^{-2}·d^{-1} stored in an overlying water mass of 30 cm for 10 d would result in an increase of 1°. This does not happen, however, so we must assume that the warmed water moves downslope rapidly, as corroborated by the dye experiments.

Freezeout

The conductance gradient across the bottom 0.5 m water is on the order of 1–2 μS (Fig. 13 and 14), or 5×10^{-9} to 10×10^{-9} g·cm^{-3}·cm^{-1} (formula 1). A temperature difference of 0.03°·cm^{-1} equals a density gradient of 1.2×10^{-6} g·cm^{-3}·cm^{-1} at 1.6°C (calculated from Kell 1975). Although the data preclude more precise comparisons, it seems that density gradients due to freezeout are much less important than gradients due to heat flow for lakes whose conductance is less than several hundred μS. Nonetheless, the increase in TDS beneath the ice must contribute to the driving force as subice water progresses shoreward, sinks, and runs downslope.

Completing the Circulation

There must be some sort of "filling up" of the deep part of a lake basin as denser water collects at $Z_{\max}$. We have not tried to quantify this aspect, but we note that the lack of temperature increase in the unfrozen lake during midwinter implies transport of warmed water upward where it loses heat to the subice surface, and that this upward heat transfer must be turbulent rather than diffusive, since molecular diffusion of heat is too slow a process to account for heat removal at the necessary rate. Also, midcolumn water near the lake center increases in salt concentration at rates too high to be the result of molecular diffusion alone (Fig. 1). However, conductance and temperature profiles taken near (but not at) the deepest part of Methane Lake, north and south basins (Fig. 10–11, 13–14), do not suggest vertical return flow. Upward circulation at the lake center, represented by the question mark in Fig. 3, is conjectural and awaits further investigation.

Acknowledgments

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Winter Respiration of Lakes at Saqvaqjuac, N.W.T.

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Welch, H. E., and M. A. Bergmann. 1985. Winter respiration of lakes at Saqvaqjuac, N.W.T. Can. J. Fish. Aquat. Sci. 42: 521–528.

Winter oxygen consumption rates at 64°N latitude were measured for 11 lake years. They ranged from 0.131 to 0.306 g $O_2 \cdot m^{-2} \cdot d^{-1}$. They were not correlated with lake depth, in contrast with the winter respiration rates of temperate lakes. We suggest that this difference results from lower summer temperatures and a lower proportion of planktonic respiration in arctic as compared with temperate lakes. ^{14}C estimates of annual photosynthesis were generally lower than estimated annual respiration, and the ^{14}C-measured photosynthesis beneath the ice in late winter was generally too low to account for the actual amounts of oxygen evolved by photosynthesis. In one lake, a 50% increase in annual production resulted in an increase of only 19% in winter respiration, suggesting that lake respiration is an integrative process that averages out production over a period of years. Addition of methane gas to simulate a gas pipeline break to a lake resulted in an immediate 67% increase in lake respiration rate.

Les taux de consommation d'oxygène à la latitude 64° N en hiver ont été quantifiés pendant 11 années-lacs. Ils variaient de 0,131 à 0,306 g $O_2 \cdot m^{-2} \cdot jour^{-1}$ et n'étaient pas en corrélation avec la profondeur du lac par opposition aux taux de respiration de lacs tempérés en hiver. Selon les auteurs, cette différence est le résultat de basses températures estivales et d'une faible proportion de respiration planctonique dans les lacs arctiques par rapport aux lacs tempérés. En général, les estimations de la photosynthèse annuelle au C^{14} étaient moins élevées que la respiration annuelle calculée et la photosynthèse, mesurée par C^{14}, sous la glace à la fin de l'hiver était généralement trop faible pour expliquer les quantités réelles d'oxygène dégagées photosynthétiquement. Dans un lac, une augmentation de 50 % de la production annuelle n'a entraîné qu'un accroissement de 19 % de la respiration hivernale, ce qui porte à croire que la respiration lacustre est un processus intégrateur qui établit une production moyenne pendant un certain nombre d'années. Une simulation de rupture d'un gazoduc par l'addition de méthane dans un lac a entraîné une augmentation immédiate de 67 % du taux de respiration lacustre.

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This work is part of a project on the experimental addition of phosphorus and nitrogen to three small lakes at Saqvaqjuac, a Department of Fisheries and Oceans Canada research site at 63°39′N, 90°39′W, 36 km north of Chesterfield Inlet hamlet on the northwest coast of Hudson Bay (Welch 1985).

At high latitudes under arctic conditions most lakes are completely sealed during winter by unbroken ice cover on top and by permafrost at the sides, such that all changes in free oxygen concentration result from internal processes. Photosynthesis is also greatly reduced or nonexistent because of the latitude effect on day length and because of heavy snow cover. At Saqvaqjuac, for example, the mean light flux penetrating the water in December ranges from 2 to 10 $\mu E \cdot m^{-2} \cdot d^{-1}$, depending upon snow cover, as compared with 900 $\mu E \cdot m^{-2} \cdot s^{-1}$ in July. In the absence of photosynthetically generated oxygen, the oxygen change therefore equals the lake's respiration. Annual lake respiration plus sedimentation (storage) thus equals autochthonous primary production plus or minus the balance between imported and exported allochthonous organic matter. Since imports and exports are low and approximately balanced at Saqvaqjuac (H. E. Welch and J. Legault, unpubl.), the winter respiration extended to a year gives an absolute lower limit to the annual autochthonous production for a lake (Welch 1974).

It is not possible to use summertime hypolimnetic oxygen depletion rates (Hutchinson 1938; Lasenby 1975; Cornett 1981) as a measure of lake respiration at this latitude because thermal stratification is either nonexistent or only weakly developed at best (H. E. Welch and J. Legault, unpubl.).

In the current work we wanted to determine normal metabolic rates for lakes in the area, and determine the response time of winter respiration in lakes that had undergone increased photosynthesis due to nutrient addition.

Methods

Description of Lakes Sampled

Routine data on hydrology, meteorology, chemistry, physical limnology, primary production, fish, and benthos were collected on four of the eight lakes included in this study: Far Lake, receiving 0.1 g P loading $\cdot m^{-2} \cdot yr^{-1}$ as H_3PO_4, 1979–83; P&N Lake, receiving 0.1 g P and 1.0 g N $\cdot m^{-2} \cdot yr^{-1}$ as $NaNO_3$, 1979–83; Jade Lake, receiving 0.2 g P and 2.0 g N $\cdot m^{-2} \cdot yr^{-1}$ 1979–80; and Spring Lake, which served as control (no treatment). The Spring Lake drainage includes a very small (3.4 ha) lake; the other three are headwater lakes, and all have simple basin morphometry. Both Jade and P&N lakes responded

TABLE 1. Respiration rates of Saqvaqjuac lakes.

Lake	Code	Year	Mean depth (m)	Winter respiration rate ($\text{g O}_2\cdot\text{m}^2\ \text{subice}^{-1}\cdot\text{d}^{-1}$)	r^2	N
Far	FA 77	1977–78	3.61	0.185	0.98	7
Far	FA 80	1980–81		0.174	0.99	8
P&N	PN 77	1977–78	3.28	0.200	1.00	6
P&N	PN 80	1980–81		0.238	0.99	8
Methane N.	MN	1977–78	4.29	0.213	0.98	9
Methane S.	MS	1977–78	5.98	0.200	0.98	13
Methane S.	—	Before CH_4 addition		0.155	0.97	4
Methane S.	—	After CH_4 addition		0.259	1.00	10
Spring	SP	1980–81	2.71	0.306	1.00	5
Jade	JA	1980–81	1.82	0.246	0.99	7
Highway	HI	1980–81	5.07	0.228	0.99	6
Hawk	HA	1980–81	11.65	0.178	0.99	6
Turkey	TU	1980–81	10.78	0.131	0.95	8

to P and N addition with increased primary production. In P&N Lake, phytoplankton photosynthesis about doubled, from a prefertilization level of 15 g $\text{C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in 1977–78 to 30 g $\text{C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in 1979–81 (H. E. Welch and J. Legault, unpubl.). Phytoplankton production did not increase in Far Lake after P-only addition.

Methane Lake, a double basin headwater lake, was divided into two separate parts during winter of 1977–78, with the South basin receiving methane gas to simulate a gas pipeline break and the North basin serving as control (Welch et al. 1980). Oxygen data were collected at that time.

The remaining lakes were sampled for oxygen only. Highway Lake is a simple basin, deep, headwater lake. Hawk Lake has a simple, deep basin with a 3.2-km^2 watershed containing several small lakes. Turkey Lake is different from the others in that it is deep, has a complex basin, and a 38-km^2 drainage which contains many other lakes. Turkey Lake has a theoretical water renewal time of about 6 mo; the others have water renewal times >1 yr.

Sampling Procedure

Samples were taken over maximum depth throughout the winters of 1977–78 and 1980–81 with a 2-L Van Dorn type sampler, 10–12 samples or 1 sample/m depth on each date, whichever was least. Glass bottles 130 mL were filled to overflowing from the bottom, flushed 3 times, stoppered, and kept cold and dark until fixed <2 h later.

Winkler oxygen determinations were essentially according to Carpenter (1965), employing 0.1 or 0.2 mol sodium thiosulphate$\cdot\text{L}^{-1}$ delivered with a 2.5-mL capacity Gilmont microburet capable of 0.0001-mL incremental additions. The titration vessel was a homemade square-sided 51-mL glass bottle with a narrow neck. In 1977–78 the end point was visual and subjective, but in 1980–81 the end point was determined photometrically (Bryan et al. 1976; Vargo and Force 1981). A beam of light passed through the titration vessel was detected by a selenium photocell, and the signal graphically amplified on a strip chart recorder. Near the end of titration, titrant was added in 0.001-mL increments at a constant rate until the asymptote was reached. The end point was taken as the intercept between a line drawn through the linear portion and a line along the asymptote, thus eliminating observer bias.

Our measured precision on titration of standards (procedure as per Carpenter 1965) was 8 $\text{mg}\cdot\text{L}^{-1} \pm \text{SE} = 0.0001$ to 0.0025; the variance on titrated samples in 1980–81 was about the same. The variance on titrated samples in 1977–78 was not much higher, but because the end point was visual and dependent on observer bias, the variance *between* sampling dates was higher for 1977–78 than for 1980–81. No overall estimate of variance is possible because we did not replicate sampling on the same date, but the high correlation coefficients for both winters (Table 1) indicates high precision for the technique during both winters.

Calculations

Freezeout of gases (exclusion of gases from freezing water) was assumed to be 100% by Welch (1974), based on a few measurements of the oxygen content of ice. During the winter of 1980–81 we made further measurements by coring large blocks of ice from known depths, melting the cores in 50-cm^3 glass syringes surrounded by water of known oxygen content, and determining the final oxygen concentration in the syringe. For clear ice we obtained 98.3% freezeout ($N = 11$) at 15 $\text{mg}\cdot\text{L}^{-1} \pm 0.0591$ SE. Therefore, in this paper we too assume 100% freezeout, an assumption that at worst yields an error of $\simeq$1% or less for lake respiration rates.

Bathymetric maps and subsequent depth:volume:area tables were prepared from transects run on calm days with a Furuno sounder (Dalton 1981). Because of the importance of the 0- to 2-m zone in ice-covered lakes, 0.5-, 1.0-, and 1.5-m isobaths were plotted from data obtained by wading out a measured distance from shore at numerous stations. The program used to compute oxygen mass balances from concentration and volume data calculated mass at 5-cm intervals between 0 and 2 m depth (the depth of maximum mean ice thickness at Saqvaqjuac), and at 1-m intervals below 2 m. The water surface in the hole was taken as 0 m. When subtracting the volume of the ice from the lake volume, the ice thickness was multiplied by 0.91 (the specific gravity of ice), e.g. 1 m of ice × 0.91 rounded to the nearest 0.05 m = 0.90 m of water whose volume was to be subtracted from the 0- to 1-m stratum.

Derivation of Correction for Freezeout and Volume Change

Assume a sealed lake with zero biochemical activity such that its total mass of O_2 is excluded by freezeout and is concentrated

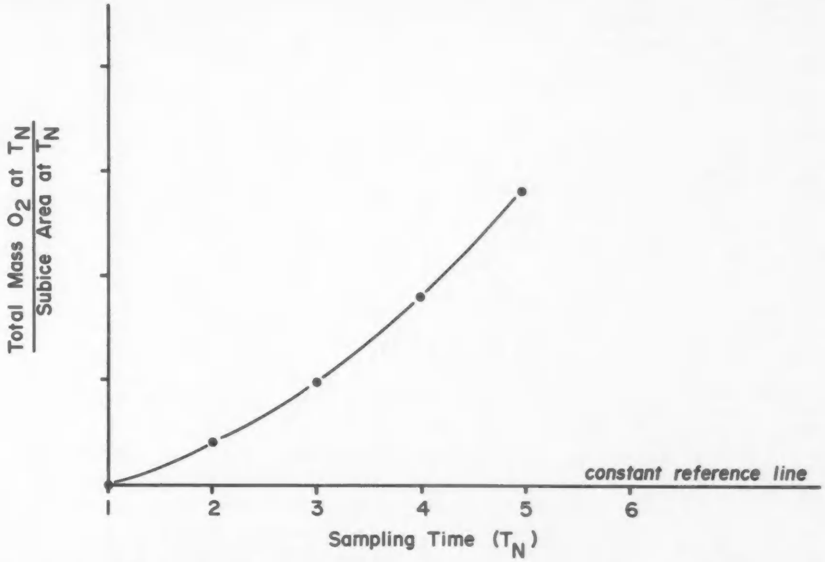

FIG. 1. Approximate curve for a hypothetical lake with zero biochemical activity, such that the mass of oxygen at any sampling time T_n is constant.

in the shrinking volume of unfrozen water. A plot of the total mass of O_2 per unit area of unfrozen lake versus time would look something like Fig. 1. By subtracting the difference between the actual O_2 mass per unit subice area at any sampling time T_n, and the mass per unit area at the initial sampling time T_1 (the constant reference level), the purely physical effects are removed, as follows:

$$(1) \quad \text{Corrected MO}\cdot\text{m}^2\,\text{AS}^{-1} = (\text{MO}_{T_n}) - \left(\frac{\text{MO}_{T_1}}{\text{AS}_{T_n}} - \frac{\text{MO}_{T_1}}{\text{AS}_{T_1}}\right)$$

where T_1 = initial sampling time, T_N = subsequent sampling time n, MO = mass of oxygen (g), and AS = subice area (m^2).

There are two components that make up the correction (the difference between the curved line and the constant reference level in Fig. 1): freezeout and volume change. Knowing the volume of new ice formed, the quantity of freezeout (the first correction) can be subtracted from the total mass of O_2 at time = n. Multiplying the original O_2 concentration at T_1 times the unfrozen lake volume at T_n, divided by the subice surface area, does not exactly correct the mass of O_2 at T_n back to the original reference point, because the mean depth of the unfrozen lake has changed (decreased, for Saqvaqjuac lakes). The difference in mean depth times the original O_2 concentration is the second correction. Combined with the freezeout correction, the result is a constant reference mass O_2 per unit area in our theoretical lake:

$$(2) \quad \text{Correct MO}\cdot\text{m}^2\,\text{AS}^{-1}$$

$$= [\text{MO}_{T_n}] - \left[\left(\frac{\text{VI}_{T_n} - \text{VI}_{T_1}}{\text{AS}}\right)(\text{O}_{T_1})\,(\text{O}_{T_1})\right] + [(Z_{T_1} - Z_{T_n})\,(\text{O}_{T_1})]$$

where VI = ice volume (m^3), Z = mean depth (m), and O_{T_1} = O_2 concentration at T_1.

The results of either procedure, using formula 1 or 2, is exactly the same: a constant reference level of O_2 per unit subice area is obtained, against which biochemical activity is shown. The slope of the regression of the corrected mass of O_2 per square meter of subice area against time is the respiration rate per unit area of unfrozen lake, and is the primary output of this paper.

To obtain the respiration rate unaffected by photosynthesis for each lake, the regression analysis uses no points after 25 March for any lake because of increasing light and resultant photosynthesis, nor data taken before 5 November in Spring, Jade, and Turkey lakes, because low snow cover on those three lakes allowed significant photosynthesis in early winter (see also discussion below).

Results and Discussion

Respiration Rates

Mean respiration in midwinter was 0.202 g $O_2\cdot m^{-2}\cdot d^{-1}$ for 10 lake years (excluding P&N, 1980–81), ranging from 0.131 for Turkey to 0.306 for Spring (Table 1). Turkey and Spring were significantly different from all other lakes (Table 2). The precision of the technique is very high if only midwinter points are used, with correlation coefficients generally 0.95 or higher (Table 1; Fig. 2).

Although a simple extrapolation of daily winter respiration to an annual basis would give a minimum estimate of annual lake respiration, such an estimate would surely be low because for about 60 summer days, Saqvaqjuac lakes average 12–14°C (H. E. Welch and J. Legault, unpubl.), or 10° higher than in winter. To calculate annual lake respirations, therefore, we have extrapolated the winter rate for 10 mo and doubled that rate for the remaining 60 d, assuming a Q_{10} of 2. Calculations were made for the unfrozen lake, summed, and expressed as per square meter of total lake surface. The annual respiration rates thus calculated range from 53 to 109 g $O_2\cdot m^{-2}$ for 11 lake years (Table 3).

TABLE 2. Significance of respiration rates between lakes. Comparison of respiration rates is based on the test for the heterogeneity of slopes (SAS package, Copyright 1982), an extension of analysis of covariance. $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$, NS = not significant ($P > 0.05$).

	SP	MS	MN	Hi	Ha	Tu	PN77	PN80	Fa77	Fa80	Ja
SP	—	***	***	***	***	***	***	***	***	***	**
MS		—	NS	NS	NS	***	NS	*	NS	*	**
Mn			—	NS	NS	***	NS	NS	NS	**	*
Hi				—	*	***	*	NS	**	**	NS
Ha					—	*	NS	**	NS	NS	**
Tu						—	**	**	**	**	***
PN77							—	*	NS	*	**
PN80								—	**	***	NS
Fa77									—	NS	***
Fa80										—	***
Ja											—

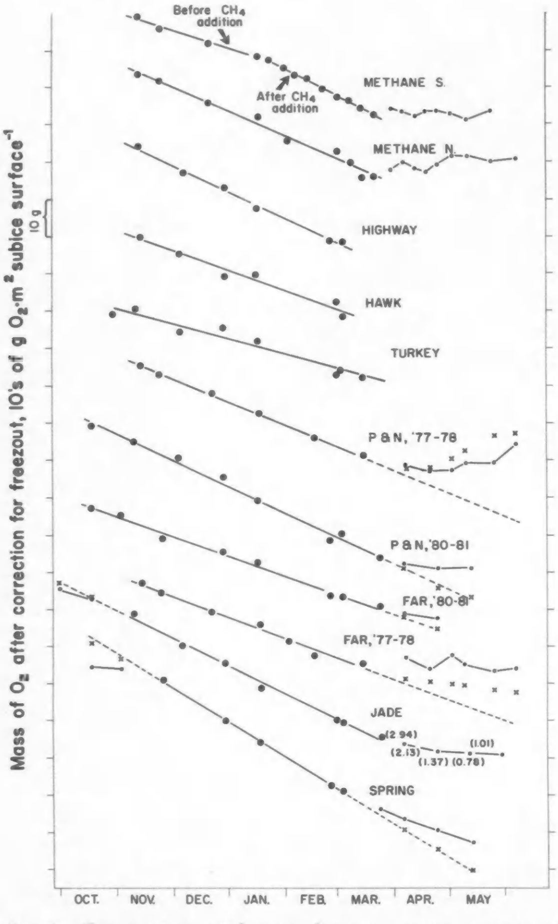

FIG. 2. Freezeout-corrected mass of oxygen per square meter of subice (= unfrozen) lake area versus time. The *y*-axis is a series of overlapping scales in 10-g increments. Curves placed only for convenience of presentation. ● = points used in regression to calculate respiration; · = other points; × = correction of extrapolated respiration rate for photosynthesis (if correct, ×'s should fall on ●'s). (Numbers in parentheses) for Jade Lake are mean oxygen concentrations by date.

Effects of Fertilization

Far Lake showed no significant changes in phytoplankton production after two years of P-only addition; as a result the pre- and post-fertilization respiration rates were not significantly different (Table 2). This is expected, since whole-lake winter respiration rates are conservative and integrate production over long periods, resulting in constant year to year rates, as was shown for undisturbed Char Lake (Welch 1974). Graneli (1979) and Barica and Mathias (1979) have also shown that primary production and carbon flux fluctuate much more than sediment respiration.

In P&N Lake by 1980, the second summer of fertilization, phytoplankton production had increased from 15.4 to 27.2 g $C \cdot m^{-2} \cdot yr^{-1}$, a 77% increase, whereas the winter respiration rate of 1980–81 showed a significant (Table 2) but relatively small increase of 19%. Although increases of organic storage in the sediments, and especially increases in summer plankton respiration as has been found at ELA (C. Kelly, Freshwater Institute, Winnipeg, Man., pers. comm.), may account for some of the difference, it appears that winter respiration lags years behind increases in lake production, and may not increase to the same degree.

In Jade Lake, although there are no prefertilization data, phytoplankton production dropped from 12.2 to 7.4 g $C \cdot m^{-2} \cdot yr^{-1}$ after fertilization was stopped (H. E. Welch and J. Legault, unpubl.), suggesting that there was an increase during fertilization. We think there was also a concomitant increase in winter respiration, because during the winter of 1980–81, oxygen became very low (mean concentration = 0.78 $mg \cdot L^{-1}$, max = 1.15 $mg \cdot L^{-1}$ on 12 May 1980), and there was mortality amongst the larger char in the lake as a result (Welch et al., unpubl.). Of course, a very small increase in respiration rate would have significant effects on total dissolved oxygen in Jade, because the mean depth in April beneath the ice is only about 1.1 m. The respiration rate in Jade remained quite constant down to about 2 mg $O_2 \cdot L^{-1}$ (Fig. 2), after which it nearly stopped. Our phytoplankton studies indicate that only about 30 mg $C \cdot m^{-2}$, or 0.08 mg $O_2 \cdot m^{-2}$, was photosynthesized 1 March to 15 May, so the decrease in respiration rate was not due to photosynthesis, but rather to low levels of dissolved oxygen. Other studies have shown that the respiration rates of small prairie lakes (Mathias and Barica 1980), lake hypolimnia (Cornett 1981; Hargrave 1972), a eutrophic arctic lake (Welch 1974), and bottom sediments (e.g. Graneli 1977) are independent of oxygen concentration above about 3 $mg \cdot L^{-1}$.

TABLE 3. Annual respiration (R) and production ($g\ O_2 \cdot m^{-2} \cdot yr^{-1}$).

Lake	Year	R	Phytoplankton photosynthesis[a]	Benthic photosynthesis[b]	Total annual photosynthesis	Photosynthesis minus respiration
Far	1977–78	67	26.7	26.5	53	−14
Far	1980–81	67	25.6	26.5	52	−15
P&N	1977–78	71	42.3	<33.6	<76	≃
P&N	1980–81	88	82.2	33.6	116	+28
Spring	1980–81	109	43.6	16.7	60	−49
Jade	1980–81	76	26.9	39.3[c]	66	−10
Hawk	1980–81	72	—	—	—	—
Turkey	1980–81	53	—	—	—	—
Highway	1980–81	92	—	—	—	—
Methane N.	1977–78	77	—	—	—	—
Methane S.	1977–78	76	—	—	—	—
		$x = 77$				
		$x = 76$ w/o P&N, 1980–81				

[a] J. Legault and H. E. Welch (unpubl.).

[b] H. E. Welch and M. A. Bergmann (unpubl.).

[c] Jade benthic photosynthesis estimate is based on only one set of samples.

Effects of CH_4 Addition

Welch et al. (1980) reported no detectable change in oxygen consumption after 110 μmol $CH_4 \cdot L^{-1}$ was added to Methane South 15 January to 25 February 1978. However, recalculation of those oxygen data using the proper freezeout correction reveals a 67% increase in respiration rate, from 0.155 g $O_2 \cdot m^{-2} \cdot d^{-1}$ before methane addition to 0.259 g $O_2 \cdot m^{-2} \cdot d^{-1}$ after addition (Table 1; Fig. 2); the difference is highly significant ($P < 0.0001$). Although the practical conclusions of Welch et al. (unpubl.) are unchanged, that a natural gas pipeline break would not result in lake anoxia, it is interesting that methane addition altered the respiration rate immediately, and the altered rate then did not change further, suggesting that there was no increase in methane-oxidizing bacteria over those that were present at the beginning of addition.

Comparison with Other Lakes

The winter respiration rates of unfertilized Saqvaqjuac lakes are only weakly correlated with mean depth ($r^2 = 0.40$; $N = 10$). This weak correlation is largely due to Turkey Lake, whose respiration rate has a relatively high variance associated with it (Table 1).

Welch (1974) also found no correlation between depth and lake respiration in the high arctic. However, the winter respiration rates of Ontario lakes (≃45°N lat.) and of small Manitoba prairie lakes are strongly correlated with mean depth (Welch et al. 1976; Barica and Mathias 1979). The only essential variable that might account for this difference is temperature, although temperature differences might affect more than one process. We suggest that the following two effects may account for the differences between mean depth:respiration rate responses noted above.

First, high arctic lakes vary in temperature less than 5°C annually (Schindler et al. 1974; H. E. Welch, pers. obs.). Saqvaqjuac lakes at 64°N have water temperatures above 7°C for only about 60 d. Both sets of arctic lakes should therefore have respiration rates that do not vary much throughout the year (see below for further discussion of this point). At 45°N, however, shallow lakes are very warm throughout for 150 d each year and must therefore respire relatively more of their annual production in summer than do deep temperate lakes with large, cold hypolimonia and a more even distribution of respiration throughout the year. The net result for temperate lakes would be a positive correlation of *winter* respiration with mean depth, whereas total *annual* respiration may have a totally different relationship to mean depth, or none at all as do arctic lakes.

Second, if plankton respiration constitutes a significant portion of winter lake respiration, the area-based respiration rates should be positively correlated with depth because deeper lakes would have more plankton respiration per square meter than shallow lakes, even if sediment respiration rates were the same. There is some evidence for this. Cornett (1981) has shown that in oligotrophic temperate lakes with shallow hypolimnia, less than 20% of the total amount of oxygen consumed in the hypolimnion is respired in the water column, whereas in deep lakes more than 60% of the total amount of oxygen consumed is respired in the water column. Mathias and Barica (1980) have also analyzed the winter respiration rates of 70 Canadian lakes by regressing volume-based oxygen depletion rates on the ration of sediment surface area:lake volume (1/mean depth). They found that for both oligotrophic and eutrophic lakes the zero intercept was about 0.01 $g \cdot m^{-3} \cdot d^{-1}$, although it was not significantly different from zero ($P > 0.05$). Such a rate would be a negligible component of lake respiration in shallow lakes but would be greater than sediment respiration rates in very deep lakes, say $Z > 20$ m.

We have plotted the Saqvaqjuac data, plus data for Char, Resolute, and Keyhole lakes (from Welch 1974), in similar fashion (Fig. 3), and find a negative rather than a positive intercept, not significantly different from zero ($P > 0.05$). These results suggest that plankton respiration is a less important component of winter respiration in arctic than in temperate lakes. This may result from the relatively long winter, the long time between peak phytoplankton photosynthesis (July–August), and the time of winter measurement (November–March), and other results of relatively low lake temperatures.

The net result of the two effects discussed above would be decreasing correlation of area-based winter respiration rates with increasing latitude.

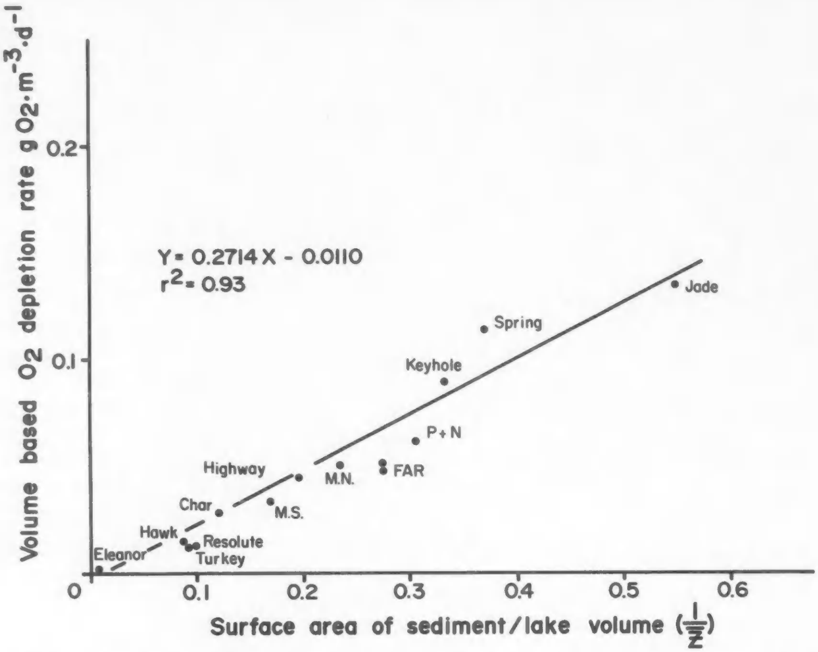

FIG. 3. Volume-based winter respiration rate versus surface area of sediment per lake volume ($1/Z$) for arctic lakes, showing lack of detectable plankton respiration.

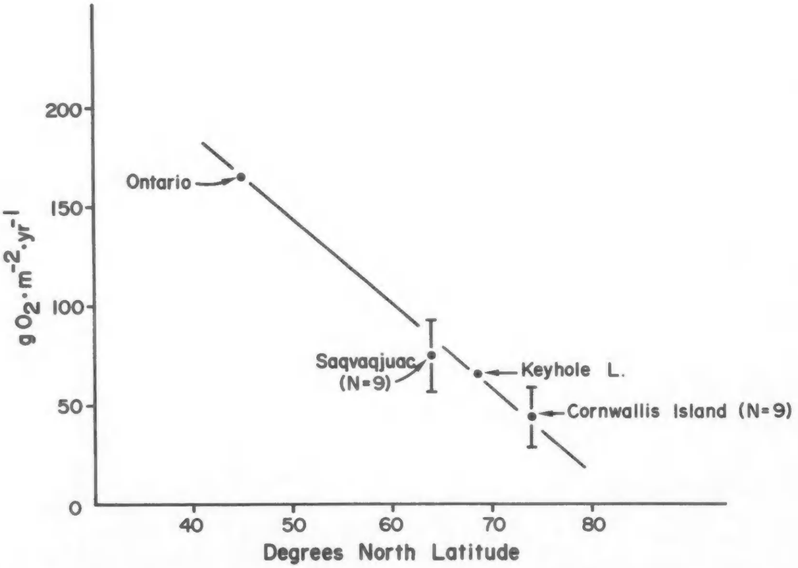

FIG. 4. Annual respiration of oligotrophic Canadian lakes as a function of latitude. Saqvaqjuac data from Table 3 ($N = 9$; ± 1 SE); Cornwallis Island and Keyhole Lake data from Welch (1974, table 1) ($N = 9$; ± 1 SE; includes Char, Resolute, Eleanor, Small, North, Barren, Plateau, Nelson, and Victory lakes). The Ontario rate is approximate and is based on a respiration rate of 0.45 g $O_2 \cdot m^{-2} \cdot d^{-1}$ or an annual primary production rate of 60 g $C \cdot m^{-2} \cdot yr^{-1}$ (see Welch et al. 1976, p. 1813, for discussion).

Latitudinal gradients

Brylinsky (1980) and Brylinsky and Mann (1973) analyzed phytoplankton production data for many lakes in the Northern Hemisphere and found that latitude was the most predictive variable. We have calculated from their figures and conversion factors that the decrease in production is about 25 g $O_2 \cdot m^{-2} \cdot yr^{-1}$ per degree of latitude for their data sets. In Fig. 4 we have plotted the arctic lakes data and indicated the general level of annual respiration for noneutrophic Ontario lakes at 45°N latitude. The change per degree of latitude is on the order of 4–5 g $O_2 \cdot m^{-2} \cdot yr^{-1}$. We suggest that the 5 times discrepancy between the two results is caused by the much wider range in lake types analyzed by Brylinsky and Mann (1973). In lower latitudes, nutrient availability results in very high productivity values for eutrophic lakes, whereas latitudinal differences between unproductive lakes is much lower, as shown by Fig. 4.

Comparison of Respiration with Photosynthesis

For four Saqvaqjuac lakes we have data on both respiration (this study), annual periphyton production (H. E. Welch and M. A. Bergmann, unpubl.), and annual phytoplankton production (H. E. Welch and J. Legault, unpubl.), although the Jade Lake periphyton production figure is based on only one sample date. Periphyton production was measured as oxygen evolution and is directly comparable with oxygen-based respiration, whereas phytoplankton production was measured using the ^{14}C incubator technique, and has been converted from carbon to oxygen equivalents using a factor of 2.75 (Winberg 1971).

In four lake years, estimated primary production was less than annual respiration, in one year it was about the same, and in one year (P&N Lake, 1980–81) photosynthesis was greater than respiration (Table 3). Considering that P&N Lake in 1980–81 had experienced about a 50% increase in production after fertilization but winter respiration increased only 19%, and that organic storage in the sediments is not taken into account, it appears that in general, either annual respiration is overestimated or photosynthesis is underestimated. Allochthonous import as total organic carbon is approximately balanced by export (H. E. Welch and J. Legault, unpubl.) and so cannot account for the discrepancy.

There is a second means of comparing whole-lake respiration and photosynthesis. In early and late winter, while the lakes are still completely sealed by ice and permafrost, enough light penetrates each lake to effect considerable photosynthesis. As a result, oxygen per square meter of subice no longer decreases linearly, but varies depending on the balance between photosynthesis and respiration (Fig. 2). It should therefore be possible to correct for oxygen evolution, which we have done. The ×'s in Fig. 2 represent the extrapolated respiration plus (in spring) or minus (in fall) the cumulative oxygen production by phytoplankton production relative to the nearest value used in the regression calculation (symbol = ·). Ideally the ×'s should predict the amount of oxygen found in the lakes; however, in all but one case the correction is low. In P&N Lake, spring 1978, the correction is somewhat high, in Far Lake, spring 1978, the correction is about 50% low, and in the remaining five cases, all for 1980–81, the correction is very low. Benthic photosynthesis might add to the total production although it is unlikely (H. E. Welch and M. A. Bergmann, unpubl.). It thus appears that phytoplankton photosynthesis is being underestimated for the ice-covered period of 1980–81.

It should be noted that verification of photosynthetic estimates in the field is extremely difficult, and arctic lakes provide a means of directly testing the assumptions inherent in measuring carbon uptake and extrapolating the results to a lake by modeling responses to light, etc. In spring especially there is ordinarily a 2- to 3-mo period when much photosynthesis can occur, which must appear on a lake's oxygen and carbon budget. Since whole-lake respiration is extremely constant, changes due to photosynthesis should be precisely detectable.

Simplification of Procedure for the Measurement of Whole-Lake Respiration

Should winter lake respiration rates be desired in the future, they may be obtained with less effort by modifying our procedures, as follows. Since the respiration rate is linear, intensive sampling may be done at two time periods only during the midwinter period, e.g. in late November and mid-February. The number of sample sets at each time can be made to correspond to the required precision; three sets of 10 samples done in 1–2 d would probably be sufficient. This reduction in sampling effort would allow a more economic sampling schedule than if the same sampling effort were distributed evenly through time.

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Physiological Smolt Characteristics of Anadromous and Non-anadromous Brook Trout (*Salvelinus fontinalis*) and Atlantic Salmon (*Salmo salar*)[1]

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McCormick, S. D., R. J. Naiman, and E. T. Montgomery. 1985. Physiological smolt characteristics of anadromous and non-anadromous brook trout (*Salvelinus fontinalis*) and Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 42: 529–538.

Anadromous brook trout, *Salvelinus fontinalis*, of rivière à la Truite, Quebec, were examined for physiological changes associated with smoltification, and compared with non-anadromous brook trout from the adjacent Matamek River. There were no statistical differences in plasma thyroxine concentration, gill Na^+,K^+-ATPase activity, hematocrit, or osmoregulatory ability between the populations. Moisture content was different between the populations, but both had the same pattern of declining moisture content as summer progressed. Silver coloration of brook trout in rivière à la Truite was associated with larger fish and higher gill Na^+,K^+-ATPase activity, but not with changes in plasma thyroxine concentrations, moisture content, hematocrit, or condition factor. Brook trout at high-salinity estuarine sites had greater gill Na^+,K^+-ATPase activity and hypoosmoregulatory ability than those from low-salinity sites. Silvering of Atlantic salmon (*Salmo salar*) in rivière à la Truite was associated with larger fish, higher gill Na^+,K^+-ATPase activity, and higher plasma thyroxine. Gill Na^+,K^+-ATPase activity of highly silvered freshwater Atlantic salmon was greater than that of highly silvered brook trout. Estuarine Atlantic salmon had significantly higher plasma thyroxine concentration and gill Na^+,K^+-ATPase activity than estuarine brook trout. Based on these physiological factors, we conclude that smoltification is undeveloped in brook trout and that estuarine residence is important for salt water acclimation and eventual seaward migration.

Les modifications physiologiques associées à la smoltification chez l'omble de fontaine (*Salvelinus fontinalis*) anadrome peuplant la rivière à la Truite (Québec) ont été étudiées et comparées à l'état physiologique de l'omble de fontaine non anadrome vivant dans la rivière Matamek avoisinante. Il n'y avait aucune différence statistique entre les populations pour ce qui est des concentrations de thyroxine dans le plasma, de l'activité du Na^+-K^+-ATP-ase dans les ouïes, de l'hématocrite et de la capacité osmorégulatoire. La teneur en humidité variait entre les populations, mais les deux montraient le même régime de décroissance de la teneur au cours de l'été. Une livrée argentée chez l'omble de fontaine de la rivière à la Truite était associée à de gros poissons et à une activité élevée du Na^+-K^+-ATP-ase dans les ouïes mais non à des variations de la concentration plasmatique de thyroxine, de la teneur en humidité, de l'hématocrite ou du facteur de condition. Les individus présents aux sites estuariens à forte salinité avaient une activité du Na^+-K^+-ATP-ase dans les ouïes et une capacité hypoosmorégulatoire plus élevées que ceux qui peuplaient les sites à faible salinité. L'argenture du saumon atlantique (*Salmo salar*) dans la rivière à la Truite était associée à de gros poissons, à une activité élevée du Na^+-K^+-ATP-ase dans les ouïes et à une concentration plasmatique élevée de thyroxine. L'activité du Na^+-K^+-ATP-ase dans les ouïes de saumons atlantiques dulçaquicoles à livrée très argentée était plus importante que chez les ombles de fontaine semblables. Les saumons atlantiques pêchés en estuaire avaient une concentration plasmatique de thyroxine et une activité du Na^+-K^+-ATP-ase significativement plus élevées que les ombles de fontaine provenant d'estuaires. D'après ces facteurs physiologiques, les auteurs formulent la conclusion que la smoltification n'est pas développée chez l'omble de fontaine et que la stabulation en estuaire est importante pour l'acclimatation à l'eau salée et la migration finale en milieu marin.

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The process of parr–smolt transformation in anadromous salmonids has received much attention in recent years owing, in part, to the realization that some aspects of artificial production may limit returns of hatchery reared smolts (Wedemeyer et al. 1980). Although comparative studies have been conducted on smolting in the genera *Salmo* and *Oncorhynchus* (see Hoar 1976 for a review), little has been reported on the possible smolt status of charrs[4] (genus *Salvelinus*). The outward signs of smolting (silvering and seaward migration), however, occur in many populations of anadromous brook trout, *Salvelinus fontinalis*, and Arctic charr (*S. alpinus*) (White 1940; Wilder 1952; Black 1981; Castonguay et al. 1982;

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[4] The spelling differs from that (char) used in *A List of Common and Scientific Names of Fishes from the United States and Canada* (American Fisheries Society Special Publication No. 12).

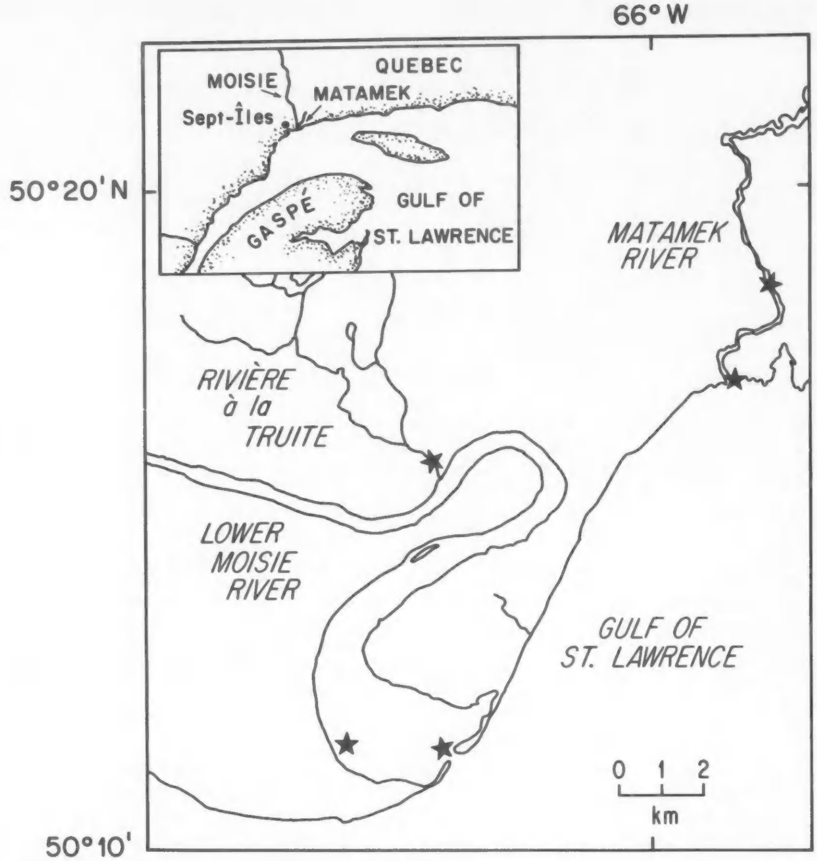

FIG. 1. Freshwater and estuarine brook trout sampling sites. Anadromous fish were captured at rivière à la Truite and at two sites in the Moisie River estuary. Non-anadromous brook trout were captured at the base of the 2nd and 3rd Falls of the Matamek River.

Nordeng 1983). The charrs are thought to be similar to the earliest anadromous salmonids (Rounsefell 1958).

Seaward migration of anadromous brook trout in northern latitudes is characterized by downstream movement in spring, residence in estuarine or coastal waters for 2–4 mo, followed by upstream migration in autumn (White 1940; Castonguay et al. 1982). Montgomery et al. (1983), studying sea-run brook trout of rivière à la Truite, found seaward migration to be temporally synchronous among individuals. In the southern portion of their range, the timing and duration of seaward migration is more variable (Mullan 1958; Smith and Saunders 1958). In addition to seasonal aspects of migration, size-dependent migration has been reported for all sea-run brook trout populations (White 1940; Wilder 1952; Smith and Saunders 1958; Dutil and Power 1980; Castonguay et al. 1982). Size-dependent and seasonal seaward migration are characteristic of all smolting salmonids (Hoar 1976). Smolting involves environmentally cued (Komourdjian et al. 1976; Grau et al. 1982), hormonally regulated changes in morphology, behavior, biochemical composition, and osmoregulatory physiology, which are presumably adaptive for seawater entry (see Hoar 1976; Folmar and Dickhoff 1980; Wedemeyer et al. 1980 for reviews). For this investigation, a smolt is defined as a freshwater salmonid that has undergone metamorphic and physiological changes preparatory for seawater entry. Prominent among these characteristics are increases in hypoosmoregulatory ability (salinity tolerance), gill Na^+,K^+-ATPase activity, plasma thyroxine (T_4), deposition of guanine and hypoxanthine on skin and scales (silvering), changes in lipid–moisture dynamics, and decreases in condition factor (Wedemeyer et al. 1980).

Knowledge of physiological changes preparing brook trout for entry into seawater would aid our understanding of anadromy in brook trout in particular, and salmonids in general, as well as upgrade the technology for sea ranching and farming of brook trout (Whoriskey et al. 1981). Our objectives were to determine if physiological changes associated with smoltification occur in northern anadromous brook trout, and if these changes are preparatory for seawater entry.

Study Sites

The Moisie and Matamek rivers empty into the Gulf of St. Lawrence approximately 22 and 36 km east of Sept-Îles, Quebec, respectively (Fig. 1). Rivière à la Truite is a 4th-order stream with an average width of 10 m and a maximum midsummer depth of 2 m that enters the Moisie River 14 km

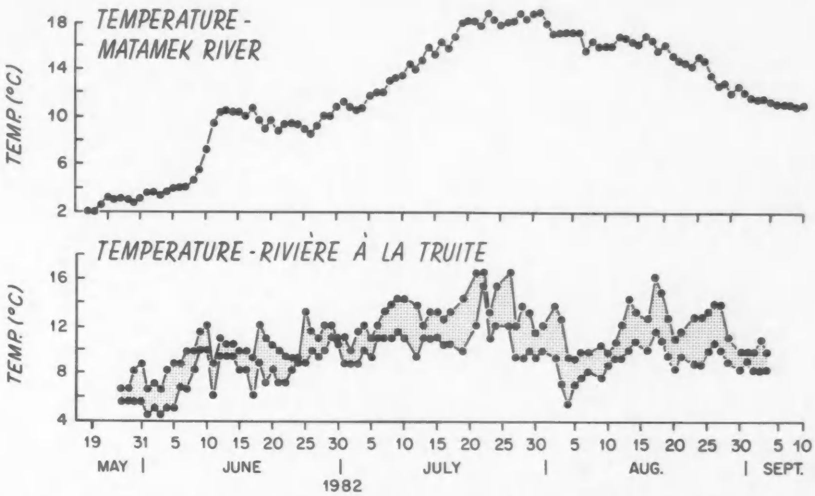

FIG. 2. Temperature profiles of rivière à la Truite (daily maximum and minimum) and the Matamek River (single day time reading) from May 19 to September 3, 1982. Ice-off occurred on May 13 and May 3 for rivière à la Truite and the Matamek River, respectively.

upstream of the Gulf of St. Lawrence. Our study site on rivière à la Truite was located 0.4 km upstream of its confluence with the Moisie River. The Moisie River broadens into a 2-km-wide estuary with sandbars restricting confluence with the Gulf of St. Lawrence to 0.25 km. Two sites were chosen in the Moisie River estuary: one 2 km upstream of the Gulf of St. Lawrence and the second at its confluence with the Gulf (Fig. 1). The Moisie River confluence site is characterized by higher salinities than the upstream site (Table 1; Montgomery 1980).

The Matamek River (6th order) averages 52 m wide and passes over five waterfalls from Matamek Lake to the Gulf of St. Lawrence (9.6 km). The 1st Falls is a barrier to upstream migration of brook trout (Haedrich 1975). Sampling of brook trout in the Matamek River occurred at the base of the 2nd and 3rd Falls. The Matamek River estuary averages 80 m wide; saline water can intrude nearly to the base of the 1st Falls. Brook trout in the Matamek River estuary have been washed over the 1st Falls and do not contribute reproductively to the river population (Haedrich 1975).

Materials and Methods

In rivière à la Truite, two fyke nets, with wings spanning the river, were placed so that one faced upstream and one faced downstream. Nets were checked and emptied daily. Details of capture methodology are reported in Montgomery et al. (1983). Fish in the Matamek River were captured by fyke nets (checked and emptied daily or every other day) or by beach seine. Seasonal temperature changes in rivière à la Truite and Matamek River are detailed in Fig. 2. Sampling of brook trout in the Moisie River estuary was accomplished with beach seines during daylight within 2 h of high tide. In the Matamek River estuary, brook trout and Atlantic salmon were sampled with beach seine at night within 2 h of high tide.

Fish were examined for degree of silvering, fork length (FL) was measured to the nearest 0.1 cm, and fish were weighed to the nearest 0.1 g. Condition factor (CF) was calculated as

$$CF = 100 \cdot \text{wet weight (g)}/\text{fork length (cm)}^3.$$

TABLE 1. Physical characteristics of Moisie River estuary and Matamek Rivery estuary sampling sites. Moisie River and Matamek River estuaries were sampled from July 2 to August 31 and June 4 to July 29, respectively. Although no salinity change was detected at the Moisie River estuary upstream site, some salt water intrusion occurs at this site and beyond (Montgomery 1980).

	Moisie River estuary		
	Upstream	Mouth	Matamek River estuary
Temperature (°C)	12–17	10–16	10–15
Salinity (‰)	0	0–27	5–27
Maximum depth (m)	6–7	6–7	5–6
Tidal influence	Yes	Yes	Yes

Degree of silvering was determined by inspection using the following criteria: (1) no silvering; (2) partial silvering, >20% of body surface reflective and silver, but parr marks or vermiculation pattern on dorsal surface clearly visible; (3) full silvering, >80% body surface is reflective and silver, parr marks or vermiculation pattern not clearly visible.

Analytical Techniques

Fish were sampled in the field within 15 min of removal from nets. Due to the difficulty of obtaining sufficient blood from small fish, only those >8.5 cm FL were used in physiological analyses. Fish were anesthetized in 0.4 mL/L phenoxyethanol solution for 30–60 s. Anesthesis for this brief period did not influence measured characteristics relative to animals stunned by a blow to the head (S. D. McCormick, unpubl. data). After anesthetization, the caudal fin was severed and blood collected into two ammonium heparinized capillary tubes. Gill arches were removed and 0.05–0.2 g (wet weight) of gill filament was trimmed from gill arches and placed in 1 mL of sucrose–EDTA–imidazole (SEI) solution (0.3 mmol/L sucrose, 0.02 mmol/L disodium ethylenediaminetetraacetate, and 0.1 mmol/L imidazole adjusted to a final pH of 7.1 with HCl). Blood and gill samples, and fish carcasses, were placed on ice and transported within 30 min to the laboratory. Hematocrit tubes were centrifuged for 5 min at 5500 rpm, hematocrit read (percent red blood cells), and plasma removed. Duplicate 25-μL plasma samples and gill samples were stored at $-17°C$ for later analysis of T_4 concentration and gill Na^+,K^+-ATPase activity.

Plasma osmolarity was measured immediately after centrifugation using a Wescor vapor pressure osmometer (intraassay coefficient of variation ±1.0%). Body moisture content (percent water) was determined by drying the central portion of the body (excluding head and tail but including viscera) at 60°C to a constant weight. Plasma T_4 was analyzed by competitive binding radioimmunoassay (Dickhoff et al. 1978). Gill Na^+,K^+-ATPase activity was determined by the method of Zaugg (1982). Details of these techniques can be found in McCormick and Naiman (1984a).

Seawater Challenge

We used a 24-h seawater challenge test (Clarke and Blackburn 1978) to measure hypoosmoregulatory ability. Gulf of St. Lawrence seawater (28‰) was supplemented with Instant Ocean salt to a salinity of 32‰ in order to provide sufficient salinity stress. Seawater challenges were conducted in a 400-L aquarium maintained at 10 ± 0.5°C, an average spring temperature for both rivers and their estuaries. To avoid overcrowding, no more than 12 fish were used in the aquarium at one time. Total ammonia levels were checked periodically and did not exceed 0.1 mg/L. Fish were transported to the laboratory within 15–45 min of capture and placed directly in the seawater aquarium. Care was taken to prevent temperature changes (±1°) or oxygen depletion during transport. After 24-h (±15 min), fish were removed from the aquarium, anesthetized in phenoxyethanol–seawater solution, and blood samples taken and analyzed as previously described.

Statistical Methods

To determine the statistical significance of physiological differences between brook trout populations, we used two-way analysis of variance (ANOVA). To determine significant differences within river populations over time, differences among fish based on silvering characteristics, and differences among estuarine brook trout and Atlantic salmon, we used one-way ANOVA. To establish homogeneity of sample variances, we used the F_{max} test. In cases where variances were heterogeneous, the data were log transformed to produce homogeneous variances. The Scheffé method was used in a posteriori tests of differences among means. Confidence level for all statistical tests was 95%, unless otherwise stated.

Results

Freshwater Studies

There was no silvering in non-anadromous brook trout of the Matamek River whereas marked silvering was observed in fish leaving rivière à la Truite ($p < 0.01$; Fig. 3). Moisture content was significantly greater in rivière à la Truite brook trout ($p < 0.01$). There were no significant differences, however, in plasma T_4, gill Na^+,K^+-ATPase activity, or hematocrit between fish from the two rivers ($p > 0.10$; Fig. 3).

Within each river, several significant changes in brook trout physiology occurred over time. Plasma T_4 levels of brook trout in rivière à la Truite were significantly higher during periods of downstream movement (May and June) than during July and August. Matamek River brook trout did not display a significant change in plasma T_4 over time. Moisture content and hematocrit had a similar pattern for fish in each river; moisture content declined with time, while hematocrit increased with time (Fig. 3). Gill Na^+,K^+-ATPase activities of brook trout in both rivers decreased over time as river temperatures increased.

To compare "smolt" appearance with "smolt" physiology, we divided brook trout from rivière à la Truite captured during the period of peak downstream migration (May 20 to June 30) into three groups based on the degree of silvering (Fig. 4). Brook trout possessing more silvering were larger ($p < 0.01$) and had higher gill Na^+,K^+-ATPase activity ($p < 0.02$). There were no significant differences in plasma T_4, moisture content, hematocrit, or condition factor among brook trout grouped by silvering ($p > 0.10$). Hematocrit and moisture content of downstream migrating fish were correlated with date of capture (day 1 = May 20, $r = 0.61$ and -0.31, $p < 0.01$ and 0.05, respectively) and were significantly correlated with one another ($r = -0.28$, $p < 0.05$, $N = 51$). With the exception of silvering, fork length did not significantly correlate with any of the measured physiological variables.

Atlantic salmon captured in rivière à la Truite were also examined for physiological smolt characteristics (Table 2). Atlantic salmon with high silvering were significantly larger and had significantly greater gill Na^+,K^+-ATPase activity and plasma T_4 than fish with intermediate and no silvering ($p < 0.05$). Hematocrit was significantly lower in highly silvered Atlantic salmon. Moisture content and condition factor were not significantly different between the two groups.

Seawater Challenge — Freshwater Fish

In rivière à la Truite, downstream migrating brook trout between 9.5 and 19.5 cm FL (13.5 ± 1.0, $x \pm$ SE) captured between June 8 and 24 were subject to a 24-h seawater challenge. Brook trout from the Matamek River (14.0–20.2 cm FL, 17.5 ± 0.7) captured between August 2 and 29 were also seawater challenged. Mean plasma osmolarity of rivière à la Truite brook trout after 24 h in seawater was 442 ± 15.7 mosmol/L ($N = 10$). This level of plasma osmolarity was not significantly different from seawater-challenged Matamek River fish (459 ± 1.35 mosmol/L; $N = 9$). Plasma osmolarity and FL of seawater-challenged fish were not significantly correlated ($p > 0.10$) in either river.

Estuarine Studies

Brook trout at the upstream site of the Moisie River estuary were significantly smaller than those from the downstream site (Fig. 5). This resulted from size dependent migration (Montgomery et al., unpubl. data). Brook trout at the mouth of the Moisie River estuary, and brook trout and Atlantic salmon in the Matamek River estuary, did not differ significantly in size (range 10.9–23.0 cm FL; Fig. 5). All fish captured at estuarine sites had silvering (either category 2 or 3); there was no significant difference in brook trout silvering between estuarine sites.

Several smolt characteristics were significantly different for brook trout and Atlantic salmon captured in estuaries. Plasma T_4 concentrations were the same for brook trout from all estuarine locations, but were significantly lower than those of Atlantic salmon from the Matamek River estuary (Fig. 5). Similarly, gill Na^+,K^+-ATPase activity was 2–3 times higher in Atlantic

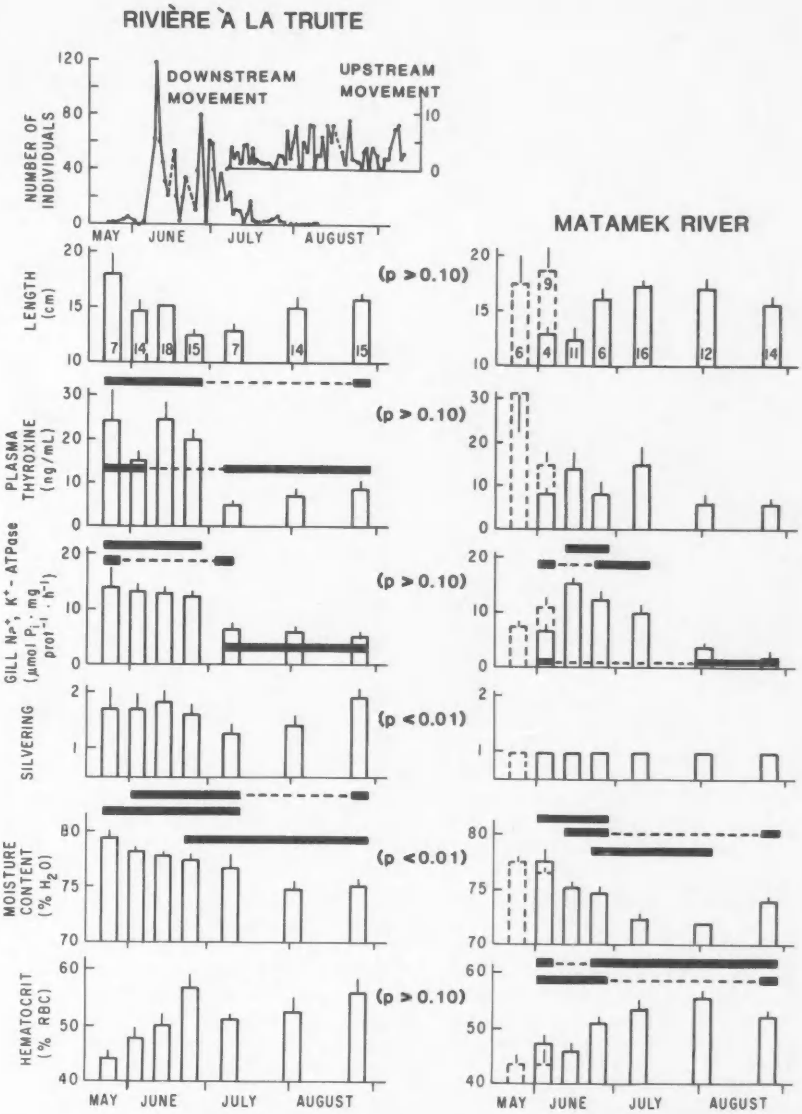

FIG. 3. Movements and physiology of anadromous brook trout in rivière à la Truite and nonmigratory brook trout of the Matamek River. Downstream and upstream movements of brook trout are daily captures of upstream and downstream facing nets. Broken lines indicate periods when the net was washed away by high water. Brook trout sampled in rivière à la Truite from late May to mid-July were moving downstream; those sampled in late July and August were moving upstream. Catches in the Matamek River did not vary greatly over the 3.5 mo of sampling, averaging one fish per day. Brook trout were divided into seven time intervals by date of capture (four 10-d, one 20-d, and two 25-d intervals), so that each time interval had approximately equal sample sizes. Dotted histograms (Matamek River) were fish captured below the 2nd Falls; solid histograms were those captured below the 3rd Falls. Only brook trout captured below the 3rd Falls were used for statistical comparisons. Sample size for each time interval is listed in the length histogram. Values are reported as $\bar{x} \pm$ SE. Statistical significance of physiological differences between brook trout populations (two-way ANOVA) is denoted by p values (in parentheses). Horizontal bars represent a posteriori differences among time interval means within rivers; intervals not connected by horizontal bars are significantly different from one another ($p < 0.05$).

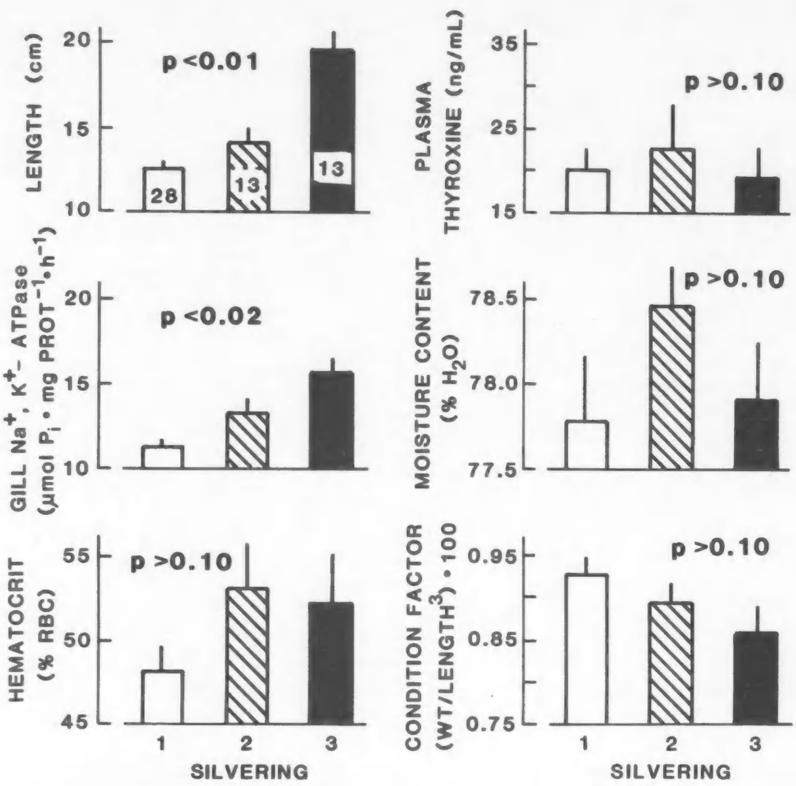

FIG. 4. Physiological comparison of brook trout migrating downstream in rivière à la Truite from May 20 to June 30. Fish were divided into three classes on the basis of silvering and compared using one-way ANOVA. Sample size is listed in the length histogram; values are reported as $\bar{x} \pm$ SE.

TABLE 2. Physiological comparison of Atlantic salmon migrating downstream in rivière à la Truite between June 6 and 29. Fish are divided into high (3) and low (1 and 2) degree of silvering on the basis of visible inspection. Values are reported as $\bar{x}$ ($\pm$ SE). Asterisks indicate significant differences between means of high and low silvering groups at $*p \leq 0.05$ and $**p \leq 0.01$ using Student's t-test.

Degree of silvering	Fork length (cm)	Gill Na^+,K^+-ATPase (µmol $P_i \cdot$ mg protein$^{-1} \cdot h^{-1}$)	Plasma thyroxine (ng/mL)	Hematocrit (% RBC)	Moisture content (% H_2O)	Condition factor $(W/L^3) \cdot 100$
Low ($N = 8$)	10.3	13.2	7.7	57	77.66	0.943
	(0.7)	(2.4)	(3.1)	(1.6)	(0.33)	(0.018)
High ($N = 6$)	12.9*	26.3*	22.7*	49**	77.94	0.928
	(0.6)	(2.4)	(6.1)	(2.4)	(0.36)	(0.008)

salmon than in estuarine brook trout. Figure 6 presents a conceptual summary of differences in gill Na^+,K^+-ATPase activity, plasma T_4, and hypoosmoregulatory ability between brook trout and Atlantic salmon.

Physiological differences also occurred among brook trout at the different estuarine sites. Gill Na^+,K^+-ATPase activities of brook trout at high-salinity sites were greater ($p < 0.05$) than at the low-salinity site. Plasma osmolarity of brook trout at the mouth of the Moisie River estuary was significantly higher than that of brook trout at the upstream Moisie River estuary site and the Matamek River estuary. Moisture content was significantly lower in brook trout at the Moisie River estuary mouth than in brook trout from the Matamek River estuary. We suggest that brook trout from the Moisie River estuary mouth were experiencing osmotic imbalance due to seawater acclimation, a process more nearly complete in brook trout from the Matamek River estuary.

Seawater Challenge — Estuarine Fish

Plasma osmolarity of brook trout from the upstream site of the Moisie River estuary was significantly higher, after seawater

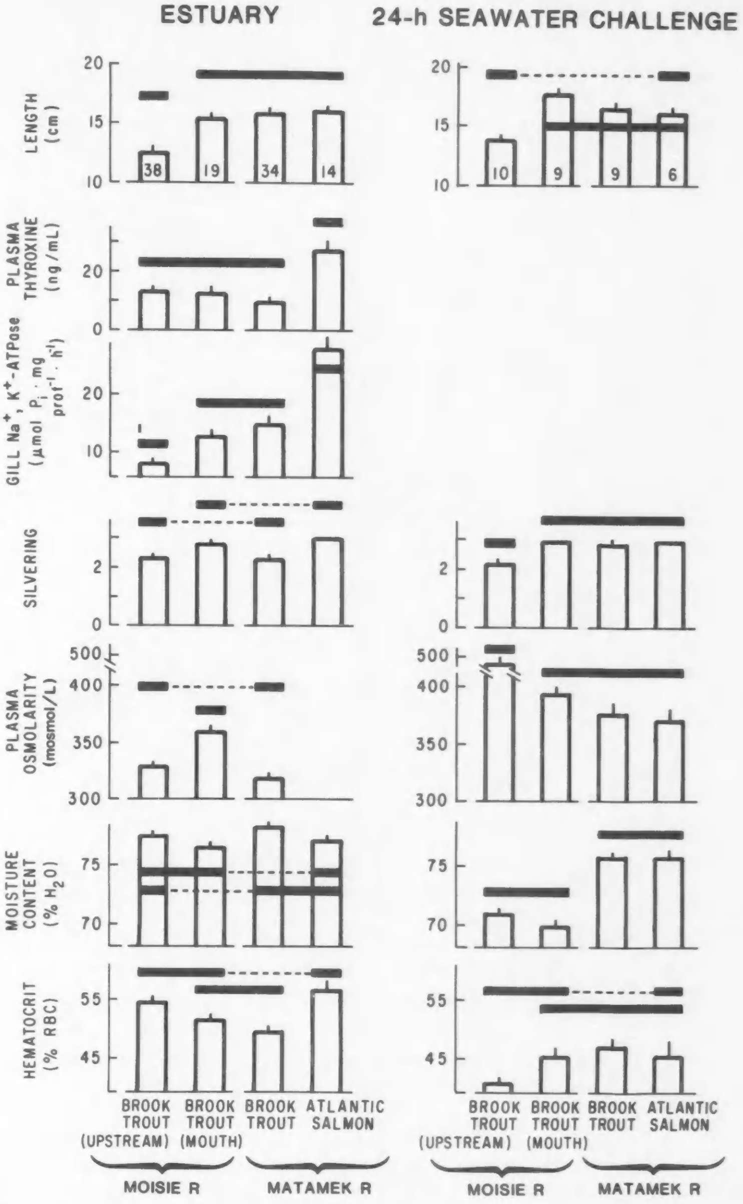

FIG. 5. Physiological comparison of brook trout and Atlantic salmon captured at estuarine sites. Brook trout were captured at one low-salinity site (Moisie River estuary, upstream) and two high-salinity sites (Moisie River estuary, mouth; Matamek River estuary). Atlantic salmon were captured in the Matamek River estuary only. Panels on the left represent sampling immediately after capture. Panels on the right report physiological changes after 24-h of exposure to seawater. Horizontal bars represent a posteriori comparison among means; groups not connected by horizontal bars are significantly different from one another ($p < 0.05$). Sample size is listed in the length histogram and is the same for all measurements. Values are reported as $\bar{x} \pm$ SE.

challenge, than that of brook trout and Atlantic salmon from the mouth of the Moisie River estuary and the Matamek River estuary (Fig. 5). Plasma osmolarity after seawater challenge was not correlated with FL for any estuarine group ($p > 0.10$). FL was significantly correlated with plasma osmolarity after seawater challenge when brook trout from all freshwater and estuarine sites were considered ($r = 0.34$, $p < 0.01$, $N = 55$). This may reflect, in part, the fact that larger fish were found at high-salinity sites. Moisture content after seawater challenge of brook trout at both Moisie River estuary sites was significantly

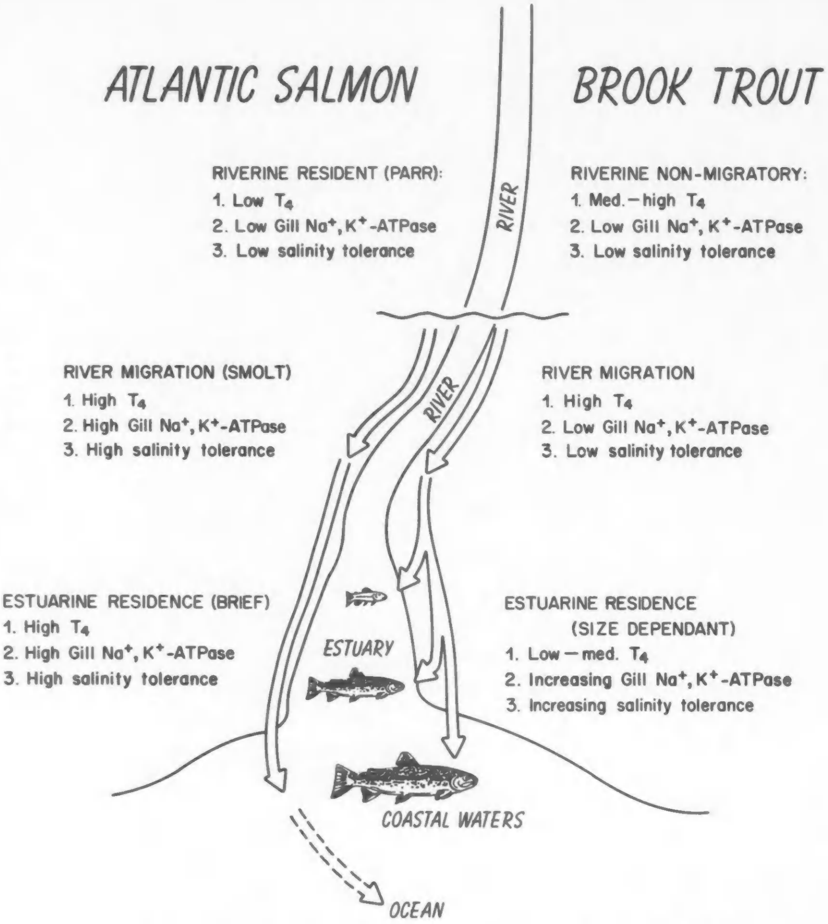
ATLANTIC SALMON
BROOK TROUT
RIVERINE RESIDENT (PARR):
1. Low T_4
2. Low Gill Na^+,K^+-ATPase
3. Low salinity tolerance
RIVER
RIVERINE NON-MIGRATORY:
1. Med.—high T_4
2. Low Gill Na^+,K^+-ATPase
3. Low salinity tolerance
RIVER MIGRATION (SMOLT)
1. High T_4
2. High Gill Na^+,K^+-ATPase
3. High salinity tolerance
RIVER
RIVER MIGRATION
1. High T_4
2. Low Gill Na^+,K^+-ATPase
3. Low salinity tolerance
ESTUARINE RESIDENCE (BRIEF)
1. High T_4
2. High Gill Na^+,K^+-ATPase
3. High salinity tolerance
ESTUARY
ESTUARINE RESIDENCE
(SIZE DEPENDANT)
1. Low — med. T_4
2. Increasing Gill Na^+,K^+-ATPase
3. Increasing salinity tolerance
COASTAL WATERS
OCEAN

FIG. 6. Conceptual model of changes in plasma T_4, gill Na^+,K^+-ATPase, and salinity tolerance of Atlantic salmon and brook trout during freshwater residence, river migration, and estuarine residence.

lower than that of brook trout and Atlantic salmon from the Matamek River estuary ($p < 0.05$).

Discussion

Wilder (1952) and McGlade and MacCrimmon (1979) studied electrophoretic, meristic, and morphometric differences of several eastern Canadian brook trout populations and concluded that anadromous and non-anadromous brook trout were a single taxonomic unit. Although Matamek River and Moisie River brook trout were found to be genetically distinct, they had greater genetic similarity than freshwater populations of brook trout examined over a broader greographic area. While these studies addressed general taxonomic characters, physiological factors associated with seaward migration may undergo stronger selection pressure resulting in genetic differences in smolt physiology.

With the exception of coloration, we found no evidence of differences in smolting physiology between anadromous and non-anadromous brook trout. Seasonal changes in plasma T_4 concentration, with high springtime values coinciding with migration, occurred in anadromous brook trout, but these changes were not significantly different from non-anadromous brook trout. Gill Na^+,K^+-ATPase activity of migratory brook trout was not different from that of non-anadromous brook trout. Salinity challenge tests of the two freshwater populations are not strictly comparable, since brook trout for this portion of the study were obtained 2 mo apart. Nonetheless, anadromous brook trout captured during the peak of migration do not appear to possess greater hypoosmoregulatory ability than non-anadromous brook trout in August, a period when the latter would not be expected to have exceptional salinity tolerance.

Although moisture content was significantly different in brook trout from rivière à la Truite and the Matamek River, each had a similar trend of decreasing levels with time. Smoltification was probably not responsible for between-river differences in moisture content. Falling moisture content and increasing hematocrit occurred through the summer, indicating that both intracellular and extracellular compartments had lower water content. Since moisture content of teleosts is inversely related to lipid levels (Phillips 1969), reduction in moisture content over time in the two populations may have resulted from greater fat deposition as food supply increased.

A seasonal cycle of high spring levels of plasma T_4 has been found in laboratory-reared brook trout that do not smoltify (McCormick and Naiman 1984a). From the absence of differences in plasma T_4 concentrations between anadromous and non-anadromous brook trout, or between anadromous brook trout of differing degrees of silvering, we suggest that the seasonal cycle of this hormone regulates functions other than migration or silvering of brook trout. We cannot rule out, however, the possibility that T_4 regulates different functions in different populations of brook trout. White and Henderson (1977) hypothesized that the seasonal T_4 cycle is involved in maturation. McCormick and Naiman (1984a, 1984c) found, however, that a 3-mo-delayed photoperiod caused a 3-mo shift in maturation but not in the T_4 cycle. Thyroxine levels were higher in fish fed maximally, and were positively correlated with differences in growth rate. Thyroid hormones have been shown to be both growth-promoting and responsive to feeding in a variety of salmonids (Flood and Eales 1983; Higgs et al. 1982). In the wild, spring increases in plasma T_4 concentration may play a role in, or result from, increased feeding or somatic growth.

Gill Na^+,K^+-ATPase activities of both rivière à la Truite and Matamek River brook trout decreased as summer progressed. Such a change in enzyme activity may be a response to increasing water temperature. Using a similar method of enzyme activity determinations, McCarty and Houston (1977) found decreases in gill Na^+,K^+-ATPase activities of rainbow trout (*Salmo gairdneri*) acclimated to high temperatures.

Of the physiological characteristics investigated, only the degree of silvering showed a clear distinction between brook trout populations in the Matamek River and rivière à la Truite. Greater silvering in rivière à la Truite brook trout is associated with greater size and increased gill Na^+,K^+-ATPase activity, characteristics that are typical of smolting salmonids (Zaugg and McLain 1972; Lasserre et al. 1978; Saunders and Henderson 1978; Buckman and Ewing 1982). The difference in gill Na^+,K^+-ATPase activity between high and no silver groups, however, was only 25%, a small value relative to differences found between salmon parr and smolt, normally 100–400% (Table 2; Folmar and Dickhoff 1980).

Black (1981) used the marine trematode *Brachyphallus crenatus*, a brook trout parasite, as an indicator of seawater residence. Brook trout captured upstream in the Moisie River estuary, though highly silvered, had only a 3% incidence of infection. Fish from the mouth of the Moisie River estuary had an 86% infection rate. Black (1981) concluded that silvering was unrelated to eventual entry into seawater. In our study, brook trout captured at the upstream Moisie River estuary site had marked silvering, but low gill Na^+,K^+-ATPase activity and hypoosmoregulatory ability. Since brook trout in the upper Moisie River estuary are similar in size to silvered fish emigrating from rivière à la Truite, it is possible that silvering is acquired during residence in the Moisie River estuary and is retained over the winter. Silvering was induced in a Matamek River brook trout maintained in 32‰ for 2 mo (S. D. McCormick, pers. obs.), and is apparently induced in brook trout washed over the 1st Falls into the Matamek River estuary.

In contrast with brook trout, Atlantic salmon captured in rivière à la Truite, and divided on the basis of silvering, showed clear indications of smoltification (Table 2). Gill Na^+,K^+-ATPase activity in highly silvered Atlantic salmon was approximately 2 times greater than Atlantic salmon with intermediate or no silvering, and plasma T_4 was 3 times greater. Plasma T_4, however, was as high for all silvering categories of rivière à la Truite brook trout as it was for highly silvered Atlantic salmon. Perhaps increased growth or activity of brook trout, irrespective of degree of silvering, can explain high plasma T_4 of brook trout during this period. Although moisture content is higher and CF is lower in highly silvered versus less silvered Atlantic salmon, the differences are not significant (Table 2). Failure to detect significant differences in these smolt characteristics may reflect differences in feeding or other environmental variables that are held constant in laboratory investigations of smolting but that are not controlled under natural conditions.

Interpretation of the estuarine physiology of brook trout must be made in light of the size-dependent migration that occurs in the Moisie River estuary. Brook trout at the Moisie River upstream site are significantly smaller than at the downstream site (Fig. 5). Brook trout >15 cm FL are rare in the Moisie River estuary, and none are >18 cm FL (Montgomery et al., unpubl. data). Large brook trout apparently leave the estuary, enter the Gulf of St. Lawrence for 2–3 mo, and return to the river in autumn. Salinity tolerance of brook trout is size dependent (McCormick and Naiman 1984b). Size-dependent salinity preference and salinity tolerance coincide in other salmonids (McInerny 1964; Weisbart 1968), and a similar phenomenon in brook trout would explain their size-dependent distribution in the Moisie River estuary.

Tagging studies have shown that Atlantic salmon smolts reside in the Matamek River estuary only 3–4 d (Gibson 1978). Coloring, body form, and physiological characteristics (Fig. 5) indicate that Atlantic salmon are fully smolted as they enter the estuary. Plasma T_4 concentrations and gill Na^+,K^+-ATPase activities of Atlantic salmon are significantly higher than estuarine brook trout. The preparatory physiological changes associated with smoltification of Atlantic salmon appear adaptive for rapid seawater acclimation and brief estuarine residence.

Gradual acclimation to seawater significantly increases seawater survival of brook trout (S. D. McCormick, unpubl. data). Activities of gill Na^+,K^+-ATPase are elevated and hypoosmoregulatory ability is greater at high-salinity estuarine sites (Fig. 5), suggesting that seawater acclimation is occurring. Whereas increases in gill Na^+,K^+-ATPase activity (and other hypoosmoregulatory mechanisms) of smolting salmonids occur wholly in freshwater, these mechanisms are apparently induced in brook trout <18 cm by estuarine residence. We suggest that the estuary is an important site for acclimation of brook trout, which ultimately permits their entry into seawater.

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Patterns of Growth and Smolting of Atlantic Salmon (*Salmo salar*) Parr in a Southwestern Newfoundland River

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A simple model of growth and smolting of Atlantic salmon (*Salmo salar*) parr, which can account for distributions of ages and lengths of random samples of sea-run smolts in Western Arm Brook, in northern Newfoundland, cannot account for distributions in Little Codroy River, in southwestern Newfoundland. Possible reasons for discrepancies include mortality dependent on growth rates, non-Gaussian growth rate distributions, and variability in individual growth rates. Smolt data do not allow us to reject any of these possibilities. Precocious maturation of male parr does not account for the discrepancies.

Un modèle simple de la croissance et de la smoltification de tacons du saumon atlantique (*Salmo salar*), qui peut expliquer la distribution des âges et des longueurs d'échantillons aléatoires de saumoneaux dévalant dans le ruisseau Western Arm (nord de Terre-Neuve), ne peut justifier la répartition dans la rivière Little Codroy (sud-ouest de Terre-Neuve). De tels écarts peuvent être causés par une mortalité tributaire des taux de croissance, les distributions du taux de croissance (autres que celles de Gauss) et la variabilité des taux de croissance individuels. Les données sur les saumoneaux ne permettent de rejeter aucune de ces possibilités. La maturité précoce des tacons mâles n'explique pas non plus ces écarts.

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To manage the stock of Atlantic salmon (*Salmo salar*) in a river, one would like to know the maximum number of smolts the river can produce. If there is a maximum number, there may be density-dependent processes that reduce parr survival, either by directly reducing the year-to-year survival of parr, or by reducing the growth rate of some parr enough to delay their smolting and subject them to stream mortality for another year. Such processes act against a background of environmental and random fluctuations in river survival. If these background fluctuations are large, density-dependent processes are difficult to document.

We have recently examined patterns in survival, growth, and smolting of parr, as revealed by sea-run smolts sampled randomly at a counting fence (Evans et al. 1984). For Western Arm Brook, a river in northern Newfoundland in which density effects appeared to be absent (Chadwick 1982a), we constructed a model that described data from 10 year-classes. The parameters of the model varied widely and most independently among the year-classes, indicating that environmental and random fluctuations were large.

Similar data are available for Little Codroy River, in southwestern Newfoundland, and we attempted to describe them with the same model. Our questions, as before, were: what can smolt data tell us about patterns of growth and smolting of parr, and how do these patterns vary? There are three possibilities: (1) the same processes are operating, at about the same levels, i.e. the Western Arm Brook model, with similar parameter values, can describe data from Little Codroy River; (2) the same processes are operating, but at different levels, i.e. the same model applies, but with very different parameter values; (3) additional processes are operating, i.e. the Western Arm Brook model cannot describe data from Little Codroy River. Evidence for additional processes will be strongest if the nature of the deviation between model and observations is the same for all or several year-classes.

There were reasons to expect that Little Codroy River differs from Western Arm Brook. At least during the early years of sampling, egg deposition per unit area of rearing habitat (including lakes) was higher in Little Codroy River. Little Codroy River had an average of 478 000 eggs (Chadwick 1982b) in 4.6 km^2 of accessible rearing habitat (Murray 1968b); Western Arm Brook had 698 000 eggs (Chadwick 1982b) in 20.5 km^2 of habitat (Chadwick and Green 1985). Parr grew faster and smolts were younger. The river is warmer: 165 d with temperatures above 7°C (Murray 1968b) compared with 149 d in Western Arm Brook (Chadwick 1982a), and therefore metabolic requirements are higher. (This is true of animals in general, and has been shown explicitly for species as closely related as chinook salmon, *Onchorhynchus tshawytscha*, juveniles (Bisson and Davis 1976).) In terms of food requirements, Little Codroy River might have an effective parr density high enough that density-dependent processes are important. Little Codroy River also has a spawning run of over 50% multi-sea-winter salmon (Murray 1968a), whereas the spawning run in Western Arm Brook is entirely one-sea-winter fish (Chadwick 1982a), and Little Codroy River has a higher proportion of precociously mature male parr.

Methods

Data and Model

Little Codroy River is a fourth-order stream in southwestern Newfoundland (approximate coordinates of mouth 47°45′N, 59°10′W). A counting fence was maintained there from 1954 to 1963. Several hundred smolts were randomly selected for measurement each year. The intensity of sampling varied, but is known for each year (Table 1). Age and length data are available for the 1952–56 year-classes (unpublished data). Essentially all smolts were age 2, 3, or 4 (Table 2).

The following model of parr growth and smolting can describe the ages and lengths of smolts from Western Arm Brook (Evans et al. 1984). A parr starts its river life with a length of 28 mm and an annual growth rate chosen at random from a Gaussian distribution whose mean MUG and standard deviation SIGG are parameters of the model. The parr grows for an integer number of years, until it has exceeded its criterion length for smolting. This length is chosen at random from a Gaussian distribution with standard deviation SIGL and a mean that varies with age: equal to MUL at age 3 and decreasing by OFFSET in each year. Parr survival is another parameter SURV; it refers only to survival past the youngest age at which parr can become smolts. We applied this model to Little Codroy River.

Statistical Tests

Given a set of parameters, the model predicts distributions of ages, and lengths within an age of sea-run smolts. We compared these with observed numbers from Little Codroy River using three nonparametric tests: the *G*-test for numbers at ages 2, 3, and 4 and two Kolmogorov–Smirnov (K–S) tests of extrinsic hypotheses for length distributions of age 2 and 3 smolts (as opposed to ages 3 and 4 for Western Arm Brook). Accepting the model as describing a year-class meant finding a set of parameters for which none of the tests showed deviations significant at the 0.05 level. Evans et al. (1984) give more details.

Rejecting the model is more difficult: it entails showing that no set of parameters can provide an acceptable fit to the data. Our technique for showing this is as follows. The growth rate parameters in the model predict distributions of lengths at a given age, ignoring the possibility of smolting. The data are of length at a given age conditional on smolting at that age. By relating absolute to conditional probabilities for length at age data, we obtain inequalities relating the model parameters to the data. We then seek some set of these inequalities that is inconsistent; if we find one, then the model must be rejected.

The *G* statistic must not be too large, and this places limits on the proportions of smolts of different ages (Evans et al. 1984). We choose π_3, the proportion of parr that would smolt at age 3 if there were no mortality, as small as possible consistent with these limits, and π_2 and π_4 as large as possible. It is easiest to satisfy other criteria with this choice, so if we can reject the model for this choice, we can reject it for any choice. Of all the restrictions on length distributions of smolts, we shall consider three. (The following abbreviations are used: $\text{obs}(L_i)$ = observed proportion of age i smolts no longer than L_i; $\text{mad}(i)$ = maximum allowed K–S deviation for the observed number of age i smolts; $\text{len}(i)$ = length a parr would attain at age i ignoring the possibility that it might smolt before then; sa = smolt age.)

TABLE 1. Total number of smolts counted in each calendar year, and the fraction (%) that was sampled.

Calendar year	Number of smolts	Sampling intensity (%)
1954	12 210	11.50
1955	11 248	10.87
1956	14 772	2.51
1957	8 900	3.29
1958	9 341	5.00
1959	12 099	5.17
1960	7 829	8.48

TABLE 2. Distribution of all the sampled smolts by age for the year classes, not corrected for differences in sampling intensity.

	Age (yr)				
Year-class	2	3	4	5	6
1952	388	650	10	0	1
1953	460	223	1	0	0
1954	131	199	15	0	0
1955	79	314	21	0	0
1956	138	459	10	0	0

First, long age 2 smolts must form a large enough fraction of all age 2 smolts; for any length L_2 we must have

(1) $P(\text{len}(2) > L_2 \mid \text{sa} = 2) \geq 1 - (\text{obs}(L_2) + \text{mad}(2)) = \Lambda_2$.

In using this requirement, we choose a length L_2 that seems likely to give trouble. Now

$$P(\text{len}(2) > L_2) = \frac{P(\text{len}(2) > L_2 \mid \text{sa} = 2)\, P(\text{sa} = 2)}{P(\text{sa} = 2 \mid \text{len}(2) > L_2)}.$$

We have set $P(\text{sa} = 2) = \pi_2$, and the denominator is a probability, ≤ 1. Therefore, using (1):

(2) $P(\text{len}(2) - L_2 > 0) \geq \Lambda_2 \pi_2$.

But $\text{len}(2) - L_2$ has the Gaussian distribution $N(28 + 2\cdot\text{MUG} - L_2, 4\cdot\text{SIGG}^2)$, so:

$$P(\text{len}(2) > L_2) = \text{P}\left[N(0, 1) > \frac{L_2 - 28 - 2\cdot\text{MUG}}{2\cdot\text{SIGG}}\right]$$

and, by (2):

(3) $\dfrac{L_2 - 28}{2} - \text{MUG} \leq \phi(\Lambda_2\pi_2)\text{SIGG} = A\cdot\text{SIGG}$

where ϕ is the inverse Gaussian integral: $\phi(x)$ is the abscissa that has an area x of $N(0, 1)$ to the right of it.

The second requirement is that long age 3 smolts form a small enough fraction of all age 3 smolts:

$$P(\text{len}(3) > L_3 \mid \text{sa} = 3) \leq 1 - (\text{obs}(L_3) - \text{mad}(3)) = \Lambda_3.$$

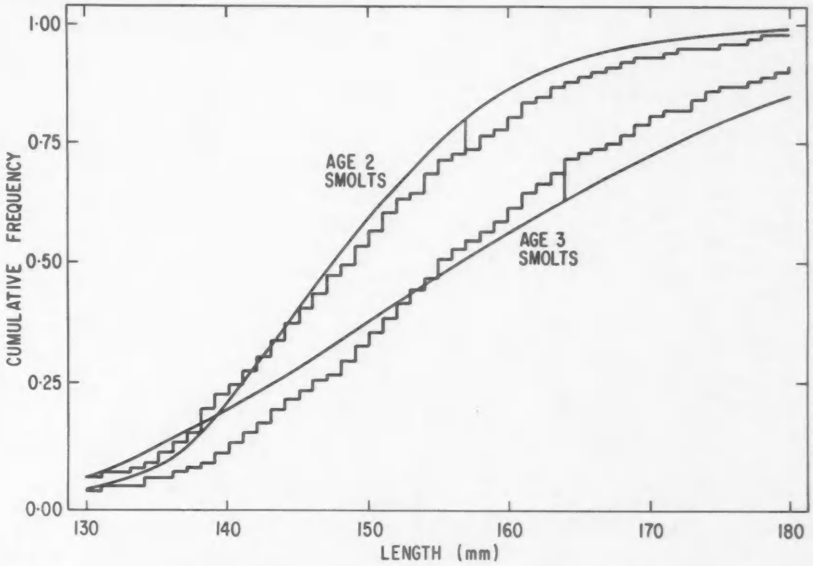

FIG. 1. Comparison of predicted (smooth line) and observed (stepped line) cumulative frequency distributions of lengths at ages 2 and 3 for the 1955 year-class. Vertical lines indicte maximum deviation.

Now,

$$P(\text{len}(3) > L_3) = P(\text{len}(3) > L_3 \mid \text{sa} = 2)\, P(\text{sa} = 2)$$
$$+\, P(\text{len}(3) > L_3 \mid \text{sa} = 3)\, P(\text{sa} = 3)$$
$$+\, P(\text{len}(3) > L_3 \mid \text{sa} = 4)\, P(\text{sa} = 4)$$

assuming that all smolts are age 2, 3, or 4.

$$P(\text{len}(3) > L_3 \mid \text{sa} = 2) \text{ is a probability, } \leq 1$$
$$P(\text{len}(3) > L_3 \mid \text{sa} = 4) \text{ is a probability, } \geq 0.$$

However, L_3 is intended as a long length for an age 3 smolt, and therefore the probability that an age 3 par is longer than L_3, given that it is not longer than its criterion length until age 4, is very small, and we shall assume that it is in fact zero. Then

$$(4) \quad P(\text{len}(3) > L_3) \leq 1 \cdot \pi_2 + \Lambda_3\pi_3 + 0 \cdot \pi_4 = \pi_2 + \Lambda_3\pi_3.$$

This last section of the appendix in Evans et al. (1984) indicates a more rigorous and delicate way to get a similar result.

The third requirement is that short age 3 smolts form a small enough fraction of all age 3 smolts. The reasoning is similar to the second requirement, except that the inequality goes the other way and so we must argue that $P(\text{len}(3) > M_3 \mid \text{sa} = 2)$ is essentially 1 if M_3 is a short length for an age 3 smolt. We then obtain

$$(5) \quad P(\text{len}(3) > M_3) \geq \pi_2 + \Omega_2\pi_3.$$

The second and third requirements together mean that the lengths of age 3 smolts should have a sufficiently narrow distribution. Turning (4) and (5) into inequalities in the parameters:

$$(6) \quad \frac{L_3 - 28}{3} - \text{MUG} \geq \phi(\pi_2 + \lambda_3\pi_2)\ \text{SIGG} = B \cdot \text{SIGG}$$

$$(7) \quad \frac{M_3 - 28}{3} - \text{MUG} \leq \phi(\pi_2 + \Omega_3\pi_3)\ \text{SIGG} = C \cdot \text{SIGG}.$$

Inequalities (6) and (7) must hold for all L_3 and M_3. It is useful to choose L_3 long enough and M_3 short enough that $B > C$ Combining (3) and (6):

$$\text{SIGG} \geq \frac{\dfrac{L_2 - 28}{2} - \dfrac{L_3 - 28}{3}}{A - B}.$$

Inequality (6) becomes

$$\text{MUG} \leq \frac{L_3 - 28}{3} - B \cdot \text{SIGG}$$

and (7) becomes

$$\text{MUG} \geq \frac{M_3 - 28}{3} - C \cdot \text{SIGG}.$$

These inequalities are potentially inconsistent. If we can choose L_2, L_3, and M_3 so that they are in fact inconsistent, then the model cannot give an acceptable representation of that year-class with any set of parameters.

Results

Parameters were found that gave an acceptable fit to the 1955 year-class. MUG was 39.1 mm/yr (the highest found for Western Arm Brook was 38.2); MUL was 131 (the lowest for Western Arm Brook was 154); SURV was 0.2; OFFSET was 0. The fit was not good: $P = 0.058$ for the lengths of age 2 smolts. The problem was that the model predicted too flat a distribution of lengths of age 3 smolts (Fig. 1). In every other year-class this feature was more pronounced, so much so that the methods described above could show no fit was possible. Figure 2 shows an attempt for the 1952 year-class.

Discussion

Compared with a model of our prior notions of what parr do in the absence of density effects, which describes all year-classes

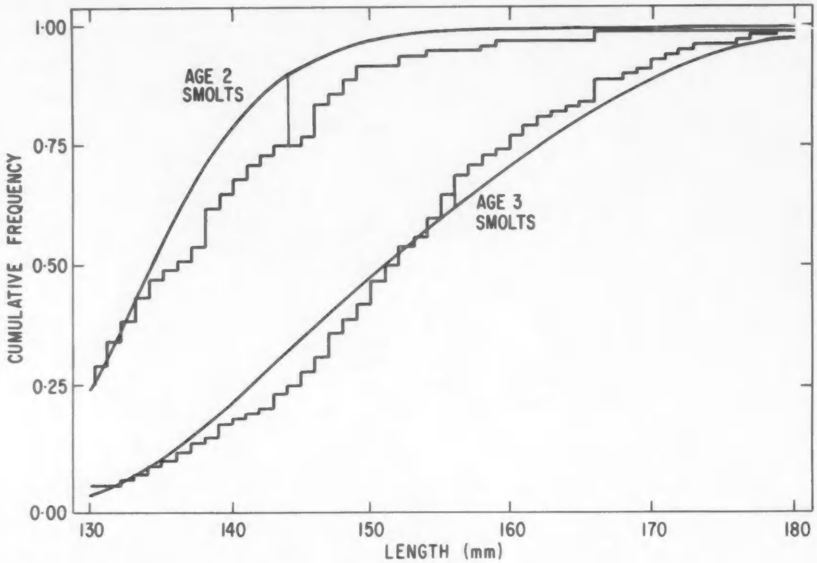

FIG. 2. Comparison of predicted (smooth line) and observed (stepped line) cumulative frequency distributions of lengths at ages 2 and 3 for the 1952 year-class. Vertical lines indicated maximum deviation.

from Western Arm Brook, age 3 smolts from Little Codroy River have an unexpectedly narrow distribution of lengths. There were two intermediate year-classes, 1955 in Little Codroy River and 1974 in Western Arm Brook, where the same deviation from the model is noticeable but not significant. The technique of subtracting a simple pattern and examining residuals reveals a more complicated pattern. However, given our sample of only two rivers, we can only speculate about causes of this new pattern.

Among possible reasons for the failure of the model to describe Little Codroy River, the most obvious and least interesting would be the added power of the tests. The samples from Little Codroy River were approximately three times as large as those from Western Arm Brook, so the tolerable deviations were smaller. This does not appear to be the reason for the lack of fits. The pattern of deviation that makes it impossible to fit Little Codroy River is not even noticeable in Western Arm Brook except in the 1974 year-class. Something different is happening at Little Codroy River.

Another suggested possibility is the effect of precocious maturation of male parr. Precociously mature males make up 15% of the smolt run in Little Codroy River, compared with 5% in Western Arm Brook (Chadwick 1982a), and their behavior as parr can invalidate the assumptions we made about growth and smolting (Myers 1984). To test this possibility, we tried to fit just female smolts with the same model, for year-classes for which we had sex data. For 1955, the model with the same parameter values described the female part of the smolt run adequately: the probabilities were higher because of the lower numbers; the form of the deviations was visibly the same. For 1954 and 1956 we can show that no fit is possible to the females. For Western Arm Brook, too, the same parameter values described the female part of the data as well as for both sexes combined. Therefore, whatever is happening is not a result of the precocious maturation of some males.

Density dependence could be invoked to account for the discrepancies. In a densely stocked river, slowly growing parr might be more likely to starve or be eaten. It seems clear that a modification of the model such that survival is less for slower growing parr could produce a steeper distribution of age 3 lengths (fewer short smolts for the same number of long ones) and therefore fit the data better. Recent high densities of parr in Western Arm Brook may enable tests of this idea.

However, parr density is only one possible systematic difference. Another possibility is that parr have a bimodal, or at least platykurtic, distribution of growth rates, as Thorpe (1977) has observed for hatchery stocks. If one of the modes was appropriate to smolting at age 2 and the other to age 3, then the length distribution of age 3 smolts would be steeper. It may be relevant that the spawning stock in Little Codroy River has a larger proportion of large salmon than Western Arm Brook, which is primarily a grilse river. Large salmon lay larger eggs than grilse (Pope et al. 1961), and parr from them may differ also. In addition, our assumption that the growth rate of a parr is constant throughout its river life is very restrictive. Almost certainly this assumption could be relaxed in ways that enable us to mimic the data.

It does not appear profitable to explore extensions of the model at this time. In our investigation of Western Arm Brook, when the original model failed we could see only one way to fix it, and the fix entailed a minimal change to the model. There is no such obvious and simple remedy here. There are, however, suggestions of more complicated patterns of growth or mortality which one might design field programs to test.

Acknowledgments

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Background Levels of Dissolved/Dispersed Petroleum Residues in the Gulf of St. Lawrence, 1970–79

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A 10-yr program of monitoring the incidence and distribution of dissolved/dispersed petroleum residues in the Gulf of St. Lawrence confirmed that the major source is the Atlantic water that enters through Cabot Strait and demonstrated that a substantial decline in the background levels occurred during the mid-1970's. The present level, about 0.4 μg/L, is similar to those of other unpolluted areas off the east coast of Canada and in the Arctic where it appears that the input from atmospheric deposition exceeds those from accidental spills, deliberate discharges, and other point sources.

Un programme décennal de contrôle de l'incidence et de la distribution des résidus pétroliers dissous ou dispersés dans le golfe du Saint-Laurent a confirmé que les eaux de l'Atlantique qui entrent par le détroit de Cabot en sont la principale source et qu'une importante baisse des niveaux ambiants a eu lieu depuis le milieu des années 1970. Le niveau actuel, qui s'élève à environ 0,4μg/L, est semblable à ceux d'autres zones non polluées au large de la côte est du Canada et dans l'Arctique, où il semble que l'apport par dépôts atmosphériques soit plus élevé que celui qui provient de déversements accidentels, de déversements intentionnels et d'autres sources.

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From a combined environmental, economic, and social point of view, the Gulf of St. Lawrence is the most important of the Canadian marginal seas and, therefore, a region where the quality of the environment must not be allowed to deteriorate. Fundamental to sound management of marine environmental quality is reliable information concerning existing concentration levels of potentially harmful substances and how these levels change with time. Since one facet of this very broad question is the incidence and distribution of dissolved/dispersed petroleum residues, a 10-yr program to monitor the concentration levels of these substances in the Gulf and the adjoining areas of the North Atlantic was carried out.

A preliminary survey of the area in 1970 indicated that the concentrations of dissolved/dispersed petroleum residues in the Gulf of St. Lawrence ranged from 1.3 to 5.5 μg/L in samples taken near the surface, at mid-depth, and near the bottom along a series of stations extending from Cabot Strait to Montreal (Levy 1971). Since there were too few data for a detailed statistical analysis, it was not possible to interpret the concentration data in terms of geographical location, depth in the water column, or any of the commonly measured oceanographic parameters. During the following year, a more detailed study demonstrated that concentrations ranged from 0 to 5 μg/L in most areas within the Gulf but that concentrations up to 18 μg/L were present in the seaward approaches to Cabot Strait (Levy and Walton 1973). Also, concentrations were generally less than 5 μg/L in the southern and western regions and between 5 and 10 μg/L in the north and east. Thus, it became clear that the concentrations of dissolved/dispersed petroleum residues in the Gulf of St. Lawrence not only had a definite geographical dependence but that the observed distribution could readily be explained in terms of the water movements in the Gulf provided that their main source was the Atlantic water that enters the region through Cabot Strait. Since this was contrary to the notion that land drainage, domestic and industrial wastes, and other sources related to man's activities in the St. Lawrence drainage basin would probably constitute the major source of oil contamination in the Gulf, the need for a better understanding of the incidence and distribution of dissolved/dispersed petroleum residues in the Gulf was clear, particularly in view of the increases expected in shipping through the Gulf, the importance of its fishery, and the likelihood of offshore oil exploration. Accordingly, with these two cruises as the starting point, a program to study the background levels of dissolved/ dispersed petroleum residues over a sufficient period to reveal long-term trends was undertaken, and another eight surveys were carried out between 1972 and 1979. From the results of these studies, a model was developed to interpret the geographical distribution of these substances. From this model, it is evident that changes that have occurred in the levels of oil contamination in the Gulf of St. Lawrence during the past decade.

Regional Setting and Physical Oceanography

The Gulf of St. Lawrence (Fig. 1) is a semi-enclosed sea, which is connected with the Atlantic Ocean by Cabot Strait (104 km wide, maximum depth 480 m) and the Strait of Belle

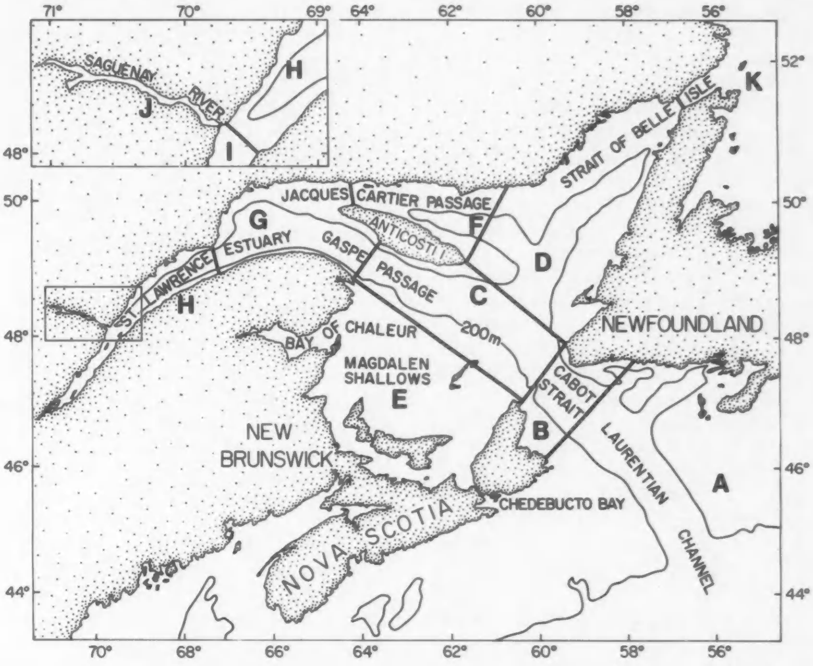

FIG. 1. An 11-compartment model of the Gulf of St. Lawrence and adjoining areas.

Isle (16 km wide, sill depth 60 m). Its most prominent bathymetric feature is the Laurentian Channel, a trench with depths generally greater than 350 m that extends from the St. Lawrence Estuary near the confluence of the Saguenay Fjord to Cabot Strait and thence 250 km across the continental shelf to the continental slope. A northeast branch of this channel extends to the Strait of Belle Isle and the Jacques Cartier Passage north of Anticosti Island.

Since the physical oceanography of the Gulf has been considered in detail in a recent review (Dickie and Trites 1983), only a very brief summary of the sources and circulation of the water in the Gulf is needed to interpret the results of this study. The saline component of the water in the Gulf is derived primarily from Labrador Current water that enters through Cabot Strait and to a much lesser extent through the Strait of Belle Isle. Freshwater enters from the St. Lawrence and a large number of small rivers which, in total, drain some $1.3 \times 10^6 \mathrm{km}^2$ of northeastern North America. Water from the southward flowing Labrador Current enters the Gulf by way of the Laurentian Channel and throughout the water column on the Newfoundland side of Cabot Strait. This water flows "upstream" with a portion of it reaching the end of the Laurentian Channel where depths change abruptly from more than 350 m to less than 40 m, and vertical mixing is sufficiently intense that the water column is often homogeneous throughout (temperature 5°C, salinity 28‰). The mixed water returns seaward above the inflowing deep water, further upwelling occurs through the Lower Estuary, a strong current forms in the Gaspé region, and the outflowing water spreads over the Magdalen Shallows before exiting on the south side of Cabot Strait. Upwelling also occurs north of Anticosti Island and around the Magdalen Islands. Superimposed on the generally counterclockwise surface circulation are transient gyres. In the deeper regions during summer, the waters of the Gulf consist of a surface layer (0–50 m, 27–32‰) that undergoes large seasonal changes in temperature, an intermediate cold layer (50–100 m, −0.5°C, 31.5–33‰) with little seasonal variability, and a deep warm layer (100 m, maximum temperature 4–6°C, 34.6‰) that fills the deeper channels and undergoes only longer term changes. This deep layer is continuous with the deeper water in the channels on the continental shelf and originates with the Labrador current. The intermediate layer is largely formed during winter when vertical mixing extends to 100–150 m and the two upper layers merge. Freshwater runoff during the spring and vernal warming give rise to the upper layer which is present during the summer. The flushing time of the freshwater in the Gulf, an important factor in terms of environmental contamination, has been estimated to be 6–8 mo (Trites 1972).

Sea ice usually begins to form locally in the St. Lawrence Estuary in early winter and in the northern and western areas of the Gulf in early January. About this time, drift ice from Labrador enters through the Strait of Belle Isle. By the end of January, the central and southwestern parts of the Gulf are covered with close pack ice, and by the end of February coverage is complete. By April, ice cover is reduced to one half over the deep areas of the Gulf, but lingers into May over the Magdalen Shallows and June in the Strait of Belle Isle.

Sampling and Analytical Methods

To ensure that the data collected during this program would not suffer from the ambiguities that would inevitably arise from changes in sampling and analytical procedures, the following techniques were used throughout.

Samples of water were collected throughout the water column, usually at standard oceanographic depths, using 5-L

Niskin samplers on a hydrographic wire or in a CTD/Rosette assembly. This procedure has been found to yield reliable results provided care is taken to avoid shipboard and other potential sources of contamination (Levy 1979a). Subsamples (1 L) were immediately extracted twice with carbon tetrachloride that had previously been shown to be free from substances that fluoresce under the conditions of analysis. Extracts were stored in the dark until returned to the Institute laboratory for analysis. After eliminating the carbon tetrachloride and any residual water, the residues were quantitatively taken up in aromatic-free hexane, and their intensities of fluorescence at 360 nm on excitation at 310 nm were compared with those from a series of solutions containing known concentrations of Bunker C fuel oil (Levy 1977). This oil, taken from the tanker *Arrow*, which grounded off the coast of Nova Scotia in 1970, has been used as the reference material throughout an extensive investigation of the background levels of dissolved/dispersed petroleum residues in the waters off the east coast of Canada (Levy 1971, 1972, 1983; Levy and Walton 1973) and in the Canadian Arctic (Levy 1979b, 1981) and ensures that the data from this laboratory do not suffer from the ambiguities that would arise from changes in reference material. For comparison with other data, the intensity of the fluorescent of this oil is 0.221 times that of chrysene under the same conditions. (A slightly modified version of this procedure has recently been recommended for studies of petroleum residues in seawater (Anonymous 1981).)

This sampling and analytical strategy not only provides a highly sensitive and economical means of processing the large numbers of samples required for meaningful studies of background levels of dissolved/dispersed petroleum residues. It also affords a means of identifying those samples that merit more detailed study using other analytical techniques, such as computerized capillary gas chromatography – mass spectrometry, to identify individual components of the residue mixture. However, because of the very low concentrations of fluorescing substances in most samples, the more sophisticated and costly analyses were not required.

Samples from the sea surface microlayer were collected during the last cruise of the program by using a modified version of the Garrett screen sampler (Garrett 1965) and processed as described above.

Because of other demands on ship time it was not possible to maintain a regular sampling schedule, or to carry out a detailed study of the entire region during every cruise. Thus, the density of sampling in the various regions differed from one cruise to another. However, this does not detract from the general conclusions concerning background levels of petroleum-related substances in the various sectors of the Gulf of St. Lawrence and the change that occurred during the period of study.

Results

During this program, data from more than 2000 samples were obtained at 448 stations during 10 oceanographic cruises conducted between 1971 and 1979.

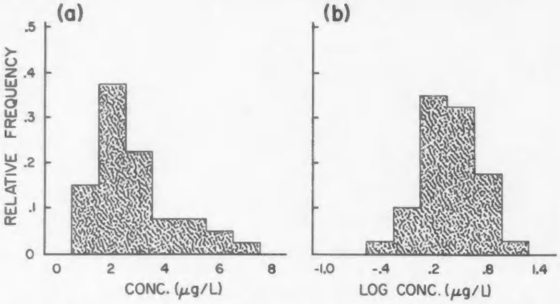

FIG. 2. Frequency distribution histograms of the (a) untransformed and (b) log-transformed concentration data from Cruise 74-028.

To facilitate the analysis of these data and interpretation of the results, the Gulf region was subdivided into 11 subareas (Fig. 1): zone A contains the source water from the North Atlantic; B comprises the water that enters the Gulf at the surface on the Newfoundland side of Cabot Strait and at depth in the Laurentian Channel and the outflowing water on the Cape Breton side; C is the central portion of the Gulf and is dominated by the deep inflowing water in the Laurentian Channel; D contains the waters of the northeastern Gulf and includes any exchange through the Strait of Belle Isle with the Atlantic (K); F is the Jacques Cartier Passage, which is the route usually taken by ships entering or leaving the Gulf through the Strait of Belle Isle; G includes a relatively permanent counterclockwise gyre in the north and the discharge from the St. Lawrence River system; E contains the water over the Magdalen Shallows; H is the lower portion of the St. Lawrence Estuary; and I and J are the upper St. Lawrence Estuary and the Saguenay Fjord.

As was the case in other studies of background levels of dissolved/dispersed petroleum residues (Levy 1983, 1981, 1979b; Levy et al. 1981), the frequency distribution histograms for the data from virtually all the cruises in the Gulf of St. Lawrence were highly skewed, with most of the values near the lower end of the range of concentrations and comparatively few at the higher. For example, the histogram for the data from cruise 74-028 (Fig. 2) indicated that almost 60% of the 530 samples contained less than 2 µg/L, with only a few of the remaining samples having concentrations greater than 5 µg/L, although a single value of 13.5 µg/L was observed. Such distributions are best analyzed after logarithmic transformation of the data (Aitchison and Brown 1969), and as illustrated by this example, the distributions for the transformed data were sufficiently close to normal in most cases to pass the χ^2-test for goodness of fit at the 95% confidence level. Consequently, the geometric mean is the appropriate measure of central tendency for the data, and, as such, provides a good estimate of the general background level existent in the region at the time. (In a few instances, the transformed data failed to satisfy the requirements of the χ^2-test at the 95% confidence level but passed at a lower level.) After calculating the background level in each zone, *t*-tests were used to evaluate the significance of any differences between adjacent zones. Where these were not statistically significant, the data were combined and the analysis was repeated. Eventually, this procedure reduced the original 11-compartment model to a much simpler one in which the differences in the background levels of dissolved/dispersed petroleum residues between adjacent zones were significant (Fig. 3).

Since the waters of the Gulf of St. Lawrence during summer consist of three relatively distinct layers, the geometric means for 50-m intervals of depth through the water column were intercompared and the geometric means for the upper 100, 200, and 300 m were compared with those for the remainder of the water column. In no instance, however, could a clear relationship between concentration and depth be established. Similarly, no direct relationship between concentration and temperature,

TABLE 1. Background levels of dissolved/dispersed petroleum residues in the Gulf of St. Lawrence, July–August 1971 (Cruise 71-027). N = number of stations; n, $\overline{\log c}$, and s are the number of samples, mean, and standard deviation, respectively, for the log-transformed concentration data; GM = geometric mean; TFC = too few classes for χ^2-test.

Region	N	n	$\overline{\log c}$	s	GM (μg/L)	χ^2-test
A. Approaches to Cabot Strait	1	3	0.801	0.775	6.32	TFC
B. Cabot Strait	7	21	0.775	0.245	5.96	TFC
C. Central Gulf	2	6	−0.069	0.275	0.85	TFC
D. Northeast Gulf	18	51	0.551	0.287	3.55	Almost passed
E. Magdalen Shallows	30	87	0.006	0.289	1.01	Passed
F. Jacques Cartier Passage	8	20	0.525	0.231	3.35	TFC
G. Gaspé Passage	14	36	0.119	0.356	1.32	TFC
H. Lower Estuary	6	18	−0.020	0.391	0.95	TFC
I. Upper Estuary	—	—	—	—	—	—
J. Saguenay River	5	15	0.441	0.235	2.75	TFC
K. Approaches to Strait of Belle Isle	—	—	—	—	—	—
Overall data set	91	263	0.259	0.406	1.82	Failed

salinity, dissolved oxygen, or nutrient concentrations was found. Thus, the observed distribution of dissolved/dispersed petroleum residues in the Gulf of St. Lawrence is not an artifact arising from natural biological or geochemical processes other than the degradation of petroleum-related substances and, therefore, can be adequately described in terms of a model based solely on oceanographic/geographic factors.

In the following analysis, the results obtained during this program are considered on a cruise-by-cruise basis. In each case, a model was derived to describe the background levels that existed in the various sectors of the Gulf at the time. While the individual models differed somewhat in detail, their general features were similar and gave rise to a general model that was applicable to the entire data set. From this general model, temporal changes in the background levels became evident.

Cruise 71-027

Although the results of this survey were reported previously (Levy and Walton 1973), a detailed interpretation of the data in terms of a general background level over a broad geographical area was not considered possible at that time because the sampling was limited to the surface, mid-depth, and near the bottom. Since then, however, the analysis of data from subsequent cruises failed to demonstrate any clear relationship in the Gulf between the concentration of dissolved/dispersed petroleum residues and depth. Consequently, the geometric means of the data from this cruise provided acceptable estimates of the background levels in the various regions at the time and thereby enabled comparison with the background levels based on data obtained from standard oceanographic depths on the later cruises.

Concentrations of dissolved/dispersed petroleum residues in the water column at this time ranged from 4 to 18 μg/L in the seaward approaches to Cabot Strait and from 0.5 to 1.0 μg/L elsewhere in the Gulf. Although there were too few values in most of the subareas to establish their statistical distribution, the geometric means indicated that the background levels were higher in Cabot Strait and seaward than those in the northeastern region and the lowest levels were in the Lower Estuary and the southwestern region (Table 1). After combining the data for those zones where the apparent differences between geometric means were not significant (i.e. zones A/B, D/F, and C/E/G/H), a four-component model that comprised the Cabot Strait area and seaward, the northeastern region, the southwestern region including the estuary, and the Saguenay Fjord emerged. The background levels in these areas were 6.0, 3.5, 1.07, and 2.75 μg/L, respectively (Fig. 3). This model, therefore, was consistent with the conclusion drawn earlier that the major source of dissolved/dispersed petroleum residues in the Gulf was Atlantic water that entered through Cabot Strait and not the discharge from the St. Lawrence and Saguenay rivers (Levy and Walton 1973).

In addition to the general survey of the Gulf, a detailed study was carried out of the area where the barge *Irving Whale* sank during the previous summer, with most of its cargo of Bunker C fuel oil (47°25.0′N; 63°19.0′W). At the time of sampling, a slick (approximately 1.5 km long and 0.5 km wide) was present, and although concentrations of unweathered oil on the sea surface exceeded those elsewhere in the Gulf (Levy and Walton 1973), the background level of dissolved/dispersed petroleum residues in the water column (geometric mean 1.2 μg/L) at this location was not significantly higher than that elsewhere on the Magdalen Shallows. Thus, while the unweathered oil on the surface of the sea indicated that oil continued to escape from the sunken barge, leakage at the existing rate was not having a detectable impact on the background level of dissolved/dispersed petroleum residues in the water column.

Finally, to examine the role of local inputs of land-based industrial wastes, samples were collected in the Saguenay Fjord and in the Bay of Chaleur. Although the background level in the Saguenay Fjord was higher than that for the adjoining estuary region, thus implying a local land-based source, any input of these materials to the Gulf via the estuary seemed to be negligible. In the Bay of Chaleur the background level (0.67 μg/L) was well below that present elsewhere on the Magdalen Shallows and, therefore, it was clear that oil-containing wastes from the forestry and mining industries in this area were not a significant source of oil contamination in the Gulf of St. Lawrence.

Cruise 72-017

During this study, sampling was focussed on the seaward

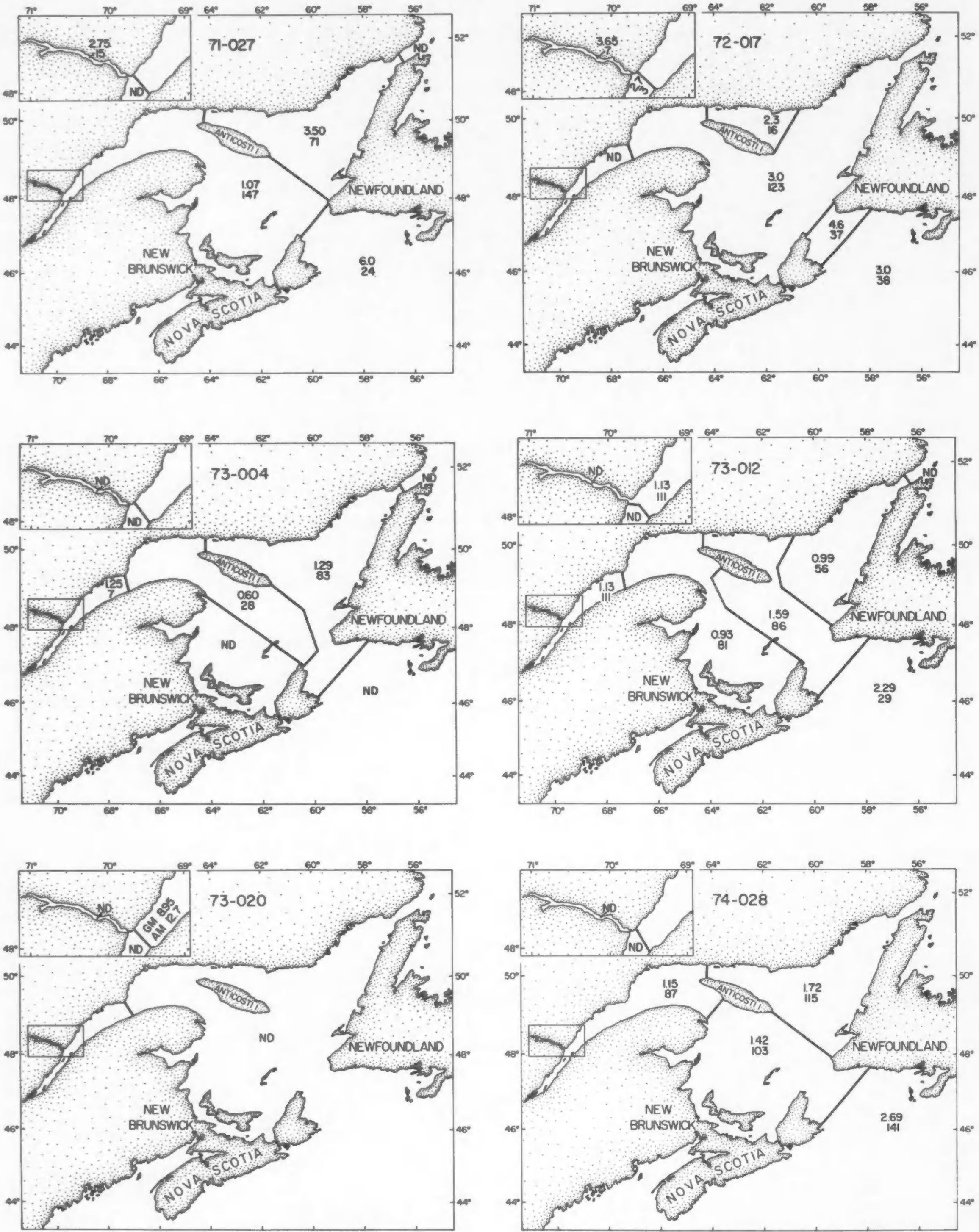
71-027
2.75
15
ND
3.50
71
1.07
147
6.0
24
ND
72-017
3.65
7
ND
2.3
16
3.0
123
4.6
37
3.0
38
73-004
ND
ND
1.25
7
0.60
28
1.29
83
ND
ND
ND
73-012
ND
1.13
111
ND
ND
1.13
111
0.99
56
1.59
86
0.93
81
2.29
29
73-020
ND
GM 8.95
AM 12.7
ND
ND
74-028
ND
ND
1.15
87
1.72
115
1.42
103
2.69
141
ANTICOSTI I.
NEWFOUNDLAND
NEW BRUNSWICK
NOVA SCOTIA
71°
70°
69°
64°
62°
60°
58°
56°
68°
66°
52°
50°
48°
46°
44°

FIG. 3. Background levels of dissolved/dispersed petroleum residues (μg/L) and number of samples in the various regions of the Gulf of St. Lawrence, 1971–79 (ND = no data available).

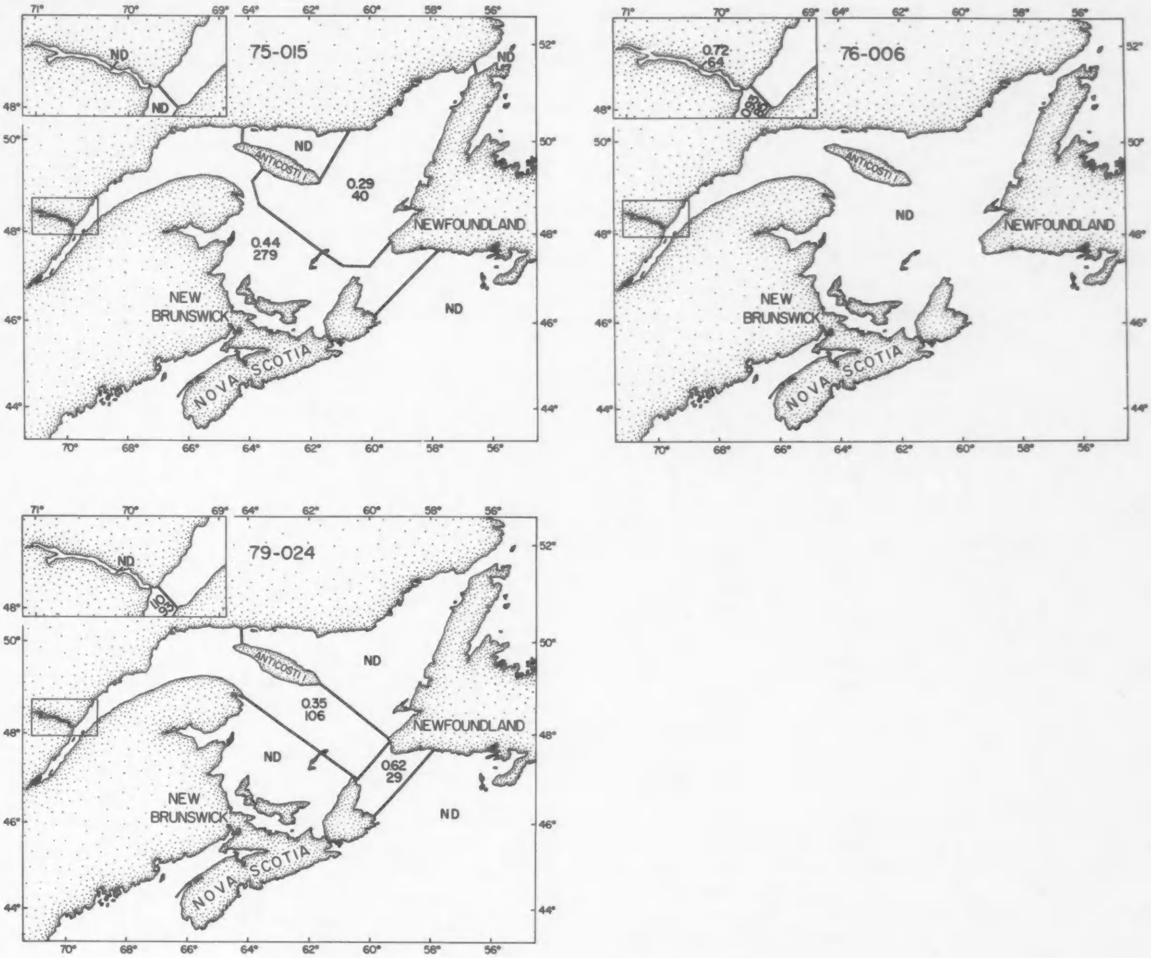
75-015
ND
ND
ND
0.29
40
0.44
279
ND
ND
ANTICOSTI I.
NEWFOUNDLAND
NEW BRUNSWICK
NOVA SCOTIA
76-006
0.72
64
0.93
ND
ANTICOSTI I.
NEWFOUNDLAND
NEW BRUNSWICK
NOVA SCOTIA
79-024
ND
1.03
9
ND
0.35
106
ND
0.62
29
ND
ANTICOSTI I.
NEWFOUNDLAND
NEW BRUNSWICK
NOVA SCOTIA
71°
70°
69°
64°
62°
60°
58°
56°
68°
66°
52°
50°
48°
46°
44°

FIG. 3. (*Concluded*)

approaches to Cabot Strait and the northeastern and Gaspé regions of the Gulf. Concentrations of dissolved/dispersed petroleum residues ranged from 0.6 to 15 μg/L in the approaches to Cabot Strait and from 0.5 to 12 μg/L in the Gulf, with more than 50% of the values between 3 and 4 μg/L. The overall data set as well as the subsets for the geographical subareas passed the χ^2-test after logarithmic transformation, and therefore, the geometric means provided a measure of the background levels of dissolved/dispersed petroleum residues in the various regions (Table 2). Since the differences between the geometric means for regions C/D, C/E, and C/G were not significant, the data for these regions were combined. Although this new set failed to pass the χ^2-test, the geometric mean indicated that the general background level for most of the Gulf at that time was 3.0 μg/L. A slightly lower level was present in the Jacques Cartier Passage, and as found in the previous study, the background level in Cabot Strait was higher than elsewhere in the Gulf. Thus, the distribution of dissolved/dispersed petroleum residues in the Gulf region at this time can be described in terms of a five-compartment model (Fig. 3) with background levels of around 3 or 4 μg/L. This uniformity was presumably a consequence of ambient oceanographic conditions, as the cruise was carried out in early spring shortly after the Gulf became ice-free and before appreciable seasonal warming had taken place. Insufficient data were available for a reliable estimate of the background levels in the Upper Estuary or Saguenay River, and the indicated difference was not statistically significant. Similarly, there were too few data for a comparison of the levels in the northeastern region of the Gulf with that in the Atlantic outside the Strait of Belle Isle.

Cruise 73-004

During this survey it was intended to cover as much of the Gulf region as possible under conditions of late winter. Heavy ice, however, precluded sampling on the Magdalen Shallows and over most of the central region.

Concentrations of dissolved/dispersed petroleum residues ranged from 0.25 to 4.6 μg/L, with most of the values around 1 μg/L. While there were too few samples in most regions to establish the statistical distribution of the data, the geometric means indicate that the background levels at that time were

TABLE 2. Background levels of dissolved/dispersed petroleum residues in the Gulf of St. Lawrence, May–June 1971 (Cruise 71-127). N = number of stations; n, $\overline{\log c}$, and s are the number of samples, mean, and standard deviation, respectively, for the log-transformed concentration data; GM = geometric mean; TFC = too few classes for χ^2-test.

Region	N	n	$\overline{\log c}$	s	GM (μg/L)	χ^2-test
A. Approaches to Cabot Strait	7	38	0.478	0.271	3.01	Passed
B. Cabot Strait	5	37	0.661	0.254	4.59	Passed
C. Central Gulf	7	35	0.410	0.311	2.57	Passed
D. Northeast Gulf	12	43	0.506	0.154	3.21	Passed
E. Magdalen Shallows	3	10	0.493	0.246	3.11	TFC
F. Jacques Cartier Passage	3	16	0.357	0.180	2.29	TFC
G. Gaspé Passage	8	35	0.506	0.184	3.21	Passed
H. Lower Estuary	—	—	—	—	—	—
I. Upper Estuary	1	3	0.436	0.034	2.73	TFC
J. Saguenay River	2	7	0.563	0.102	3.65	TFC
K. Approaches to Strait of Belle Isle	1	3	0.355	0.094	2.25	TFC
Overall data set	49	227	0.499	0.242	3.15	Passed

relatively uniform throughout the region with perhaps slightly higher levels in Cabot Strait and the northeastern regions than elsewhere (Table 3). Since the differences between the geometric means for zones B/D, D/F, and C/G were not significant, the data for these areas were combined to produce a three-component model, namely, the northeastern, central, and estuary regions, wherein the background levels of dissolved/dispersed petroleum residues were 1.3, 0.60, and 1.3 μg/L, respectively (Fig. 3).

Cruise 73-012

This survey provided one of the most thorough studies of the Gulf of St. Lawrence with detailed coverage of all zones except the Upper Estuary and the region seaward of the Strait of Belle Isle. Concentrations of dissolved/dispersed petroleum residues ranged from 0.3 to 7.5 μg/L, and when sorted geographically, the data for all zones passed the χ^2-test after transformation, except for E and F where there were too few data for a meaningful test (Table 4). Since the differences between their geometric means were not significant, the data for Cabot Strait, the central portion of the Gulf, and the Jacques Cartier Passage were combined and the resulting background level for the region at the time was 1.6 μg/L. Similarly, the data for the Gaspé and Magdalen Shallows areas were combined (0.93 μg/L), as were those for the Lower Estuary and the Saguenay Fjord (1.13 μg/L). In this case, then, background levels in the Gulf region could be described in terms of five compartments, namely, the Lower Estuary and Saguenay, the Gaspé and Magdalen Shallows, the northeastern region, the central region, and the approaches to Cabot Strait. As before, the highest concentrations were seaward of Cabot Strait and lowest in the northeastern and southwestern regions.

As found during an earlier survey (Cruise 71-027), the concentration level (0.91 μg/L) at the site where the *Irving Whale* sank did not exceed that for the other locations sampled on the Magdalen Shallows, and therefore, there was again no evidence that the sunken barge was giving rise to elevated concentrations of dissolved/dispersed petroleum residues in the water column. In addition, the concentrations in the Cornerbrook – Bay of Islands area, which receives domestic and industrial wastes from the town and a pulp and paper mill, were no higher than elsewhere in the northeastern region, indicating that inputs from these potential sources were not having a noticeable effect on the general background levels in the area.

Cruise 73-020

This was a very brief survey to investigate the impact on the background level of dissolved/dispersed petroleum residues in the Lower Estuary from a spill of Bunker C fuel oil from the collision on July 4, 1973, between the bulk carrier *Florence* and the tanker *St. Spyridon* in the lower St. Lawrence Estuary. At the time of sampling, the floating oil and associated slicks on the sea surface were being moved back and forth by the strong tidal currents in this area but with a net transport downstream. Near the site where the incident occurred, concentrations of dissolved/dispersed petroleum residues in the upper 50 m of the water column ranged from 6.5 to 95.5 μg/L but decreased to 5.0–7.0 μg/L some 60 km downstream. Although there were too few data for a rigorous statistical treatment, the impact of the spill on the background level of dissolved/dispersed petroleum residues in the Estuary was evident. Not only were the average concentrations (arithmetic mean 12.7 μg/L, geometric mean 9.0 μg/L) (Fig. 3) much higher than those observed before the spill, but also the variability was much greater because of the nonhomogeneous distribution of the oil in the water column. Since this was a very small spill, it is unlikely that it had any impact on background levels in the Gulf region as a whole.

Cruise 74-028

Sampling during this cruise covered all areas of the Gulf except the Upper Estuary and the Saguenay River. Special attention was given to the approaches to Cabot Strait and the Strait of Belle Isle to compare background levels in the Gulf with those outside. In addition, two fjords, Bay d'Espoir and Bonne Bay, on the south and west coasts of Newfoundland were sampled.

Concentrations ranged from 0.2 to 7.9 μg/L in the Gulf, 0.5 to 13.5 μg/L in the approaches to Cabot Strait, and 0.5 to 4 μg/L in the approaches to the Strait of Belle Isle. The data sets for the entire region and the various geographical subareas were lognormally distributed, and the geometric means for the various areas ranged from 1.1 μg/L in the Gaspé Passage to 2.7 μg/L in the approaches to Cabot Strait (Table 5). Since the

TABLE 3. Background levels of dissolved/dispersed petroleum residues in the Gulf of St. Lawrence, February–March 1973 (Cruise 73-004). N = number of stations; n, $\overline{\log c}$, and s are the number of samples, mean, and standard deviation, respectively, for the log-transformed concentration data; GM = geometric mean; TFC = too few classes for χ^2-test.

Region	N	n	$\overline{\log c}$	s	GM (μg/L)	χ^2-test
A. Approaches to Cabot Strait	—	—	—	—	—	—
B. Cabot Strait	6	33	0.138	0.235	1.37	TFC
C. Central Gulf	2	10	−0.330	0.304	0.47	TFC
D. Northeast Gulf	9	42	0.106	0.260	1.29	Passed
E. Magdalen Shallows	—	—	—	—	—	—
F. Jacques Cartier Passage	2	8	0.035	0.289	1.09	TFC
G. Gaspé Passage	5	18	−0.167	0.254	0.69	TFC
H. Lower Estuary	2	7	0.099	0.255	1.25	TFC
I. Upper Estuary	—	—	—	—	—	—
J. Saguenay River	—	—	—	—	—	—
K. Approaches to Strait of Belle Isle	—	—	—	—	—	—
Overall data set	26	123	0.036	0.293	1.09	Failed

TABLE 4. Background levels of dissolved/dispersed petroleum residues in the Gulf of St. Lawrence, April–May 1973 (Cruise 73-012). N = number of stations; n, $\overline{\log c}$, and s are the number of samples, mean, and standard deviation, respectively, for the log-transformed concentration data; GM = geometric mean; TFC = too few classes for χ^2-test.

Region	N	n	$\overline{\log c}$	s	GM (μg/L)	χ^2-test
A. Approaches to Cabot Strait	5	29	0.359	0.349	2.29	Passed
B. Cabot Strait	6	34	0.196	0.247	1.57	Passed
C. Central Gulf	7	37	0.190	0.200	1.55	Passed
D. Northeast Gulf	12	56	−0.007	0.204	0.99	Passed
E. Magdalen Shallows	5	19	−0.003	0.236	0.99	TFC
F. Jacques Cartier Passage	3	15	0.243	0.264	1.75	TFC
G. Gaspé Passage	12	62	−0.041	0.200	0.91	Passed
H. Lower Estuary	17	78	0.269	0.229	1.85	Passed
I. Upper Estuary	—	—	—	—	—	—
J. Saguenay River	8	33	0.180	0.243	1.51	Passed
K. Approaches to Strait of Belle Isle	—	—	—	—	—	—
Overall data set	75	389	0.154	0.301	1.43	Almost

differences in background levels between zones B/C/E, D/F, and G/H were not statistically significant, the data for these zones were combined to produce a five-compartment model consisting of the approaches to Cabot Strait, the southern Gulf, the northern Gulf, the St. Lawrence Estuary – Gaspé area, and the approaches to the Strait of Belle Isle (Fig. 3). Concentration levels were highest in the approaches to Cabot Strait, intermediate in the central portion of the Gulf, and lowest in the St. Lawrence Estuary – Gaspé Passage area. As in the previous cruises, the background level in the Atlantic outside Cabot Strait was significantly higher than that in the Gulf, thereby providing still further support that the Atlantic waters were the main source of dissolved/dispersed petroleum residues in the Gulf of St. Lawrence. On the other hand, the background level in the Atlantic outside the Strait of Belle Isle was slightly lower than that in the northeastern portion of the Gulf. The difference between the background level in the Atlantic in the Strait of Belle Isle region and that in the region south of Newfoundland was primarily a consequence of oceanographic factors. In the former region, the water is predominantly arctic water that flows southward along the Labrador shelf whereas the water in the latter is a complex mixture of Labrador current water, Slope water, and outflow from the Gulf of St. Lawrence. Thus the similarity between the background levels in the northeastern portion of the Gulf and that in the Atlantic near the Strait of Belle Isle was a result of the exchange and mixing of Gulf and Atlantic waters in this region. In the Atlantic south of Newfoundland, however, not only is there much more ship activity but the Slope water in this area is thought to be the main source of dissolved/dispersed petroleum residues both here and on the Grand Banks (Levy 1983).

Concentrations in the isolated Newfoundland fjords (Bonne Bay, 1.51 μg/L; Bay d'Espoir, 1.99 μg/L) were lower than those in the adjoining waters to the seaward, but the difference between the levels in the two fjords was not significant.

Cruise 75-015

Sampling during this survey was focussed on the Gaspé region, although coverage was also good in Cabot Strait and the Lower Estuary. In addition, samples were collected from five stations in the Bay of Islands, Newfoundland, to provide additional information about this body of water.

Concentrations were less than 1 μg/L in nearly all the

TABLE 5. Background levels of dissolved/dispersed petroleum residues in the Gulf of St. Lawrence, July–August 1974 (Cruise 74-028). N = number of stations; n, $\overline{\log c}$, and s are the number of samples, mean, and standard deviation, respectively, for the log-transformed concentration data; GM = geometric mean; TFC = too few classes for χ^2-test.

Region	N	n	$\overline{\log c}$	s	GM (μg/L)	χ^2-test
A. Approaches to Cabot Strait	16	141	0.428	0.271	2.69	Passed
B. Cabot Strait	7	44	0.173	0.314	1.49	Passed
C. Central Gulf	4	25	0.117	0.190	1.31	TFC
D. Northeast Gulf	15	83	0.258	0.334	1.81	Passed
E. Magdalen Shallows	5	34	0.147	0.238	1.40	Passed
F. Jacques Cartier Passage	6	32	0.178	0.378	1.51	Passed
G. Gaspé Passage	13	64	0.054	0.223	1.13	Passed
H. Lower Estuary	5	23	0.082	0.337	1.21	Passed
I. Upper Estuary	—	—	—	—	—	—
J. Saguenay River	—	—	—	—	—	—
K. Approaches to Strait of Belle Isle	6	31	0.108	0.258	1.29	Passed
Overall data set	77	530	0.235	0.315	1.72	Passed

TABLE 6. Background levels of dissolved/dispersed petroleum residues in the Gulf of St. Lawrence, May–June 1975 (Cruise 75-015). N = number of stations; n, $\overline{\log c}$, and s are the number of samples, mean, and standard deviation, respectively, for the log-transformed concentration data; GM = geometric mean; TFC = too few classes for χ^2-test.

Region	N	n	$\overline{\log c}$	s	GM (μg/L)	χ^2-test
A. Approaches to Cabot Strait	—	—	—	—	—	—
B. Cabot Strait	7	62	−0.398	0.240	0.40	Passed
C. Central Gulf	2	14	−0.578	0.215	0.25	TFC
D. Northeast Gulf	5	26	−0.544	0.189	0.29	Passed
E. Magdalen Shallows	4	24	−0.385	0.154	0.41	TFC
F. Jacques Cartier Passage	—	—	—	—	—	—
G. Gaspé Passage	19	144	−0.329	0.257	0.47	Failed
H. Lower Estuary	5	49	−0.365	0.205	0.43	Passed
I. Upper Estuary	—	—	—	—	—	—
J. Saguenay River	—	—	—	—	—	—
K. Approaches to Strait of Belle Isle	—	—	—	—	—	—
Overall data set	42	348	−0.386	—	—	Failed

samples collected during this cruise, although one sample contained more than 11 μg/L. The data from this cruise were unique, however, in that the frequency distribution histograms for the overall data set and for the Gaspé region contained an exceptionally large number of values in the central portion of a very narrow range of concentrations. Consequently, neither the untransformed nor the log-transformed data passed the χ^2-test, and it was not clear whether the arithmetic or the geometric mean provided the more appropriate measure of the background level. However, since they were almost identical, this is of no practical consequence. The distributions for the other subareas of the Gulf were lognormal wherever sufficient data were available for a meaningful χ^2-test.

The background levels for the various subareas of the Gulf of St. Lawrence during this cruise were not only remarkably uniform but also were much lower than those observed during the previous cruises (Table 6). Since the means for areas B/E/G/H and C/D were not significantly different, the data were combined to produce a two-compartment model of the Gulf (Fig. 3) in which the background levels were 0.44 and 0.29 μg/L. Although the difference in the background levels for these two areas were statistically significant, such a small difference can hardly be expected to have any environmental meaning, since the backgrounds are sufficiently below the concentrations of dissolved/dispersed petroleum residues that are known to have toxic effects or have been found to have sublethal effects on marine life (Kiceniuk and Khan 1983).

The concentration level in the Bay of Islands area of Newfoundland did not differ from that of the northeastern portion of the Gulf, and therefore, the data confirm the results of an earlier study which indicated that neither the town of Cornerbrook nor its paper mill was having a detectable influence on the concentrations of dissolved/dispersed petroleum residues in the Gulf.

Cruise 76-006

Since this cruise was restricted to the Upper Estuary and the Saguenay Fjord, it afforded an opportunity for studying the concentrations of dissolved/dispersed petroleum residues in the regions where freshwater from the St. Lawrence and Saguenay rivers mix with seawater from the Laurentian Channel. Concen-

TABLE 7. Background levels of dissolved/dispersed petroleum residues in the Gulf of St. Lawrence, August–September 1979 (Cruise 79-024). N = number of stations; n, $\overline{\log c}$, and s are the number of samples, mean, and standard deviation, respectively, for the log-transformed concentration data; GM = geometric mean; TFC = too few classes for χ^2-test.

Region	N	n	$\overline{\log c}$	s	GM (μg/L)	χ^2-test
A. Approaches to Cabot Strait	—	—	—	—	—	—
B. Cabot Strait	3	29	−0.210	0.190	0.62	TFC
C. Central Gulf	1	12	−0.509	0.177	0.31	TFC
D. Northeast Gulf	—	—	—	—	—	—
E. Magdalen Shallows	—	—	—	—	—	—
F. Jacques Cartier Passage	—	—	—	—	—	—
G. Gaspé Passage	10	58	−0.427	0.248	0.37	Passed
H. Lower Estuary	4	36	−0.453	0.182	0.35	Passed
I. Upper Estuary	30	93	0.043	0.270	1.10	Passed
J. Saguenay River	—	—	—	—	—	—
K. Approaches to Strait of Belle Isle	—	—	—	—	—	—
Overall data set	48	231	−0.207	0.338	0.62	Almost passed

trations in the Saguenay Fjord ranged from 0.35 to 8.75 μg/L (arithmetic mean 0.94 μg/L, geometric mean 0.72 μg/L) (Fig. 3), with most of the higher values clustered near the upper reaches of the fjord. The substantially higher concentrations (arithmetic mean 1.37 μg/L, geometric mean 0.92 μg/L) in this area compared with those in the remainder of the fjord clearly indicated the impact of local domestic and industrial inputs of nonpolar aromatic substances to this area. Similarly, concentrations in the freshwater-dominated portion of the Upper Estuary were substantially higher than those farther downstream (arithmetic mean 2.02 μg/L, geometric mean 1.67 μg/L versus arithmetic mean 0.77 μg/L, geometric mean 0.65 μg/L). Thus, in both areas the influences of inputs associated with the river discharges were detected. However, these were very localized because of "removal" processes associated with the mixing of the fresh and saline waters such as the scavenging of organic substances by suspended particulate matter and its subsequent settling from the water column.

Cruise 79-024

The sampling program in this case was focussed on the Estuary and Gaspé areas with the result that sampling was sparse in Cabot Strait and only one station was occupied in the central region. In addition to the water column, the sea surface microlayer was sampled at 37 stations.

Concentrations in the water column during this cruise ranged from 0.1 to 7.5 μg/L, with by far the most of the values less than 0.5 μg/L. Because of this clustering, the overall data set after log transformation failed to pass the χ^2-test. However, when the data were sorted geographically, the subsets for the Gaspé, Upper Estuary, and Lower Estuary regions passed, while there were too few data from Cabot Strait and the central Gulf for meaningful tests. On this basis, the background levels were slightly greater than 1 μg/L in the Upper Estuary and somewhat less in the other regions sampled (Table 7). Since the differences between the geometric means for zones C/G and G/H were not significant, these were combined to provide a three component model. The background level in the Upper Estuary was 1.1 μg/L, in the central Gulf 0.35 μg/L, and in Cabot Strait 0.62 μg/L (Fig. 3).

Concentrations of dissolved/dispersed petroleum residues in the sea surface microlayer in the Gulf of St. Lawrence at this time ranged from 10 to over 160 μg/L, but only a few values exceeded 50 μg/L. Since the log-transformed data passed the χ^2-test, the geometric mean of 22 μg/L indicated that the general level of surface contamination was about an order of magnitude higher than the concentration in the underlying water column. This is consistent with the relationships between similar sets of data for Baffin Bay (Levy 1981, 1979b) and the Grand Banks (Levy 1983). It is noteworthy, also, that the highest levels of surface contamination were in the Cabot Strait area and at the entrance to the St. Lawrence Estuary.

Discussion

A Comprehensive Model

The foregoing analysis demonstrated that the incidence and distribution of dissolved/dispersed petroleum residues in the waters of the Gulf of St. Lawrence and adjoining areas during the period 1970–79 could be interpreted in terms of general background levels pertaining to "boxes" of water defined solely on the basis of oceanographic/geographic regimes. Since no relationship could be found between the concentration of these substances and depth or any of the other commonly measured oceanographic parameters and because the apparent differences between the concentration levels in neighboring boxes often were not significant, the background levels in the Gulf region at the time of each cruise could be accounted for by a simple model with four or five compartments.

Since the general features of those models were very similar, only minor modifications were needed to produce a four-compartment model that adequately described the background levels throughout the region for the entire period of study. In this model, which consists of the approaches to Cabot Strait, Cabot Strait, Gulf, and Lower Estuary (zones A, B, C/D/E/F/G, and H of the model shown in Fig. 1), water in the Gulf exchanges with both the Lower Estuary and Cabot Strait. The water in Cabot Strait, in turn, interacts with the Gulf and the Atlantic. On the other hand, the Atlantic beyond the Strait of Belle Isle (zone K) is not included, as no significant difference was noted between the background levels in the northeastern portion of the Gulf and the Atlantic approaches to the Strait of Belle Isle and

TABLE 8. Background levels of dissolved/dispersed petroleum residues in the Gulf of St. Lawrence, 1971–79: simplified model illustrating temporal changes (μg/L). Numbers in parentheses are the number of values included in the geometric means.

Dates	Approaches to Cabot Strait	Cabot Strait	Gulf	Lower Estuary	Cruise
July–Aug. 1971	6.3 (3)	6.0 (21)	1.6 (200)	0.95 (18)	71-027
May–June 1972	3.0 (38)	4.6 (37)	2.9 (139)	—	72-017
Feb.–Mar.	—	1.4 (33)	0.95 (78)	1.3 (7)	73-004
Apr.–May	2.3 (29)	1.6 (34)	1.1 (189)	1.9 (78)	73-012
July–Aug. 1974	2.7 (141)	1.5 (44)	1.45 (238)	1.2 (23)	74-028
May–June 1975	—	0.40 (62)	0.42 (250)	0.43 (49)	75-015
Aug.–Sept. 1979	—	0.62 (29)	0.35 (70)	0.35 (36)	79-024

there is little net exchange of water between the Gulf and the Atlantic through this passage (Garrett and Petrie 1981). Similarly, the Upper Estuary and Saguenay regions (zones I and J) are not included because any input from these regions to the Gulf must occur by way of the Lower Estuary.

When the data were reanalyzed from this point of view, the general relationships between the background levels of dissolved/dispersed petroleum residues in the various geographic/oceanographic domains as described previously stood out more clearly (Table 8). For example, in three of the four cases where there were data, the background level in the approaches to Cabot Strait was greater than that in Cabot Strait, and in six of the seven cases the level in Cabot Strait was greater than that in the Gulf. On the other hand, there was no consistent trend between the levels in the Gulf and those in the Lower Estuary.

Temporal Trends

As with the individual models, this general model endorsed the concept that the major source of these substances in the Gulf is the influx of Atlantic water through Cabot Strait, that inputs associated with the discharge from the St. Lawrence drainage basin are negligible by comparison, and that no substantial exchange occurs through the Strait of Belle Isle. Within the Gulf the background levels in the various regions are closely related to the major circulation pattern. Thus, the key to managing environmental quality of the Gulf of St. Lawrence region insofar as dissolved/dispersed petroleum residues are concerned lies in the control of the input of these substances to the North Atlantic, particularly in the approaches to Cabot Strait and, at the same time, avoiding any increase in direct local inputs.

More significant than the actual values of the background levels and this geographical distribution, however, is the decrease in background levels that occurred throughout the region during the early 1970's (Table 8), and by 1975 a "steady state" seemed to have been reached between the rate of input and the ability of the Gulf to "assimilate" dissolved/dispersed petroleum residues. While the cause of this decline is not known, it is tempting to surmise that it was brought about largely by measures taken during the late 1960's and early 1970's to prohibit the discharge of oil into the Gulf of St. Lawrence and to limit discharges on the high seas areas. (The possibility of this decline being a procedural artifact is unlikely, as care was taken to use the same sampling and analytical procedures throughout the study.) Although clandestine discharges of oily wastes continue to occur, any decrease in the background level in the Atlantic approaches to Cabot Strait would soon be manifest by changes in the background levels in the Gulf because of the 6–8 mo residence time (Trites 1972) for water in the Gulf. Thus, the observed decrease in the background levels of dissolved/dispersed petroleum residues in the Gulf of St. Lawrence might very well reflect the efficiency of pollution control measures in arresting environmental deterioration and improving environmental quality in a semienclosed sea such as the Gulf of St. Lawrence. (It is, of course, not possible from the data presently available to detect seasonal effects related to spring runoff, winter ice conditions, or other changes that occur on a time scale shorter than the residence time.)

While the most recent detailed survey of the Gulf was made in 1979, data collected in 1981 at one station in the Laurentian Channel south of Newfoundland indicated that the background level in the source water for the Gulf was 0.63 μg/L (Levy 1983). This is in excellent agreement with the level measured in Cabot Strait in 1979 and implies that the background level in the Gulf itself was probably similar, or perhaps even somewhat lower, than that observed in 1979. Thus, the environmentally positive trend towards lower levels of contamination by dissolved/dispersed petroleum residues had apparently not been reversed.

Source Material

The present background level of dissolved/dispersed petroleum residues in the Gulf of St. Lawrence is similar to those of the Grand Banks (Levy 1983) and Baffin Bay (Levy 1981) and the Hudson Strait – Labrador shelf regions (E. M. Levy, unpubl. results), none of which receives large direct inputs of petroleum residues from anthropogenic sources. Since the concentrations throughout these remote regions were very uniform, it has been postulated that the dissolved/dispersed petroleum residues were derived primarily from a diffuse source such as fallout from the atmosphere of nonpolar aromatic substances formed during the high-temperature combustion of organic materials. Because the concentrations of dissolved/dispersed petroleum residues in the Gulf during the last few surveys were also very uniform and of the same magnitude, it seems likely that a substantial portion of the present background in the Gulf is similarly derived. Thus, point sources such as discharges from ships or other direct anthropogenic inputs, which were probably the major source in the past, have become a comparatively smaller portion of the total input during the past decade.

Although small spills such as those resulting from the sinking of the *Irving Whale* and the collision between the *Florence* and *St. Spyridon* occur occasionally, their effects are usually local and short-term and have little, if any, lasting impact on the regional levels. Similarly, inputs of petroleum residues from land-based sources around the Gulf are presently insignificant except at the extreme upper reaches of the St. Lawrence Estuary and the Saguenay Fjord. Even there, however, the effect is highly localized because of dilution, sedimentation, and other processes of removal associated with the mixing of fresh and saline waters, and therefore, these sources do not make a significant contribution to the background level in the Gulf region as a whole.

Conclusion

A 10-yr program of investigating the incidence and distribution of dissolved/dispersed petroleum residues in the Gulf of St. Lawrence demonstrated a decline in background levels to those in remote, presumably pristine, marine waters of northern Canada. Since the existing background levels in all these regions are well below those known to have immediate and direct adverse effects on marine life, there is no reason at present for environmental alarm. Neither, however, is there room for complacency, since any increase in the rate of input could easily alter the present situation, possibly with serious deterioration of environmental quality. As a result, monitoring of the background levels of dissolved/dispersed petroleum residues in the Gulf of St. Lawrence and elsewhere should be carried out from time to time in the future.

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Rates of Food Exploitation by Littoral Fishes in a Mesotrophic North-Temperate Lake

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Boisclair, D., and W. C. Leggett. 1985. Rates of food exploitation by littoral fishes in a mestrophic north-temperate lake. Can. J. Fish. Aquat. Sci. 42: 556–566.

The relationship between the biomass of food consumed by the littoral zone fish community of Lake Memphremagog, Quebec, and the total biomass of littoral zone food present was estimated on a daily and annual basis. The dominant food consumed were benthic invertebrates followed by forage fishes and plankton. The daily geometric mean exploitation rate was 0.55% of the total dry weight food biomass in the littoral zone. The corresponding annual rate was 72%. Energy equivalents were 0.81% (daily) and 105% (annual). When benthic invertebrate biomass values were adjusted to more accurately reflect availability (on the basis of depth distribution in the sediments and size) the geometric mean dry weight exploitation rates were 0.80% (daily) and 104% (annual). Corresponding energy rates were 1.15% (daily) and 150% (annual). These rates are significantly lower than reported benthic *P*/*B* ratios for 21 north-temperate lakes. These data indicate that littoral zone fishes crop only a very small fraction of the food biomass in the littoral zone. We conclude that the behaviors of both predator and prey act to limit the *available* fraction of the total food biomass and predict that the ratio of available to total food biomass in the littoral zone of north-temperate lakes will approximate 1%. This is consistent with existing empirical models linking fish production/biomass with biomass at lower trophic levels.

La relation entre la biomasse de nourriture consommée par la communauté de poissons du lac Memphrémagog, Québec, et la biomasse totale de nourriture présente dans la zone littorale a été estimée sur une base journalière et annuelle. La nourriture consommée a été dominée par les invertébrés benthiques suivis des poissons et du plancton. La moyenne géométrique du taux d'exploitation journalier a été de 0,55 % du total de la biomasse sèche dans la zone littorale. Le taux annuel correspondant a été 72 %. Les équivalents énergétiques ont été 0,81 % (journalier) et 105 % (annuel). Quand les biomasses d'invertébrés benthiques ont été ajustées pour mieux refléter la disponibilité (sur la base de la distribution verticale dans les sédiments et de la taille) les moyennes géométriques des taux d'exploitation poids secs ont été 0,80 % (journalièrement) et 104 % (annuellement). Les taux énergetiques correspondant ont été 1,15 % (journalièrement) et 150 % (annuellement). Ces taux sont significativement plus petits que les rapports *P*/*B* pour les invertébrés benthiques de 21 lacs nord-tempérés. Ces données indiquent que les poissons consomment seulement une très faible fraction de la biomasse de nourriture dans la zone littorale. Nous concluons que les comportements des prédateurs et des proies agissent pour limiter la fraction *disponible* de la biomasse totale de nourriture, et prédisons que le rapport de la biomasse disponible sur la biomasse totale de nourriture dans la zone littorale des lacs nord-tempérés sera approximativement 1 %. Ceci est en accord avec les modèles empiriques existant qui relient la production/biomasse de poissons avec la biomasse des niveaux trophiques inférieurs.

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The annual rate of fish production and/or the total fish biomass in lakes has repeatedly been shown to be related to lake depth (Northcote and Larkin 1956; Rawson 1960; Ryder 1965; Ryder et al. 1974; Matuszek 1978; Hanson and Leggett 1982; Prepas 1983). Both Ryder et al. (1974) and Hanson and Leggett (1982) have speculated that the mean depth variable is an indirect measure of littoral zone area. Northcote and Larkin (1956) provided estimates of the ratio of littoral zone area (<10 m depth profile) to mean depth for 100 primarily oligotrophic British Columbia lakes. Their data reveal a strong negative correlation ($r^2 = 0.88$) between percent littoral zone area (Y) and mean depth ($\bar{z}$) ($Y = 381.6\bar{z}^{-0.95}$). We developed a similar but independent data set for 28 widely distributed North American lakes representing a broader range of trophy. We also found a strong negative correlation ($r^2 = 0.79$) between littoral zone area (<5 m depth profile) and mean depth ($Y = 166.0\bar{z}^{-0.74}$).

These relationships, together with the previously described empirical links between mean depth and fish production/biomass, suggest that the magnitude and efficiency of the transfer from littoral zone food energy to fish may be a major determinant of fish production and biomass in lakes. This hypothesis is supported by the higher production at all trophic levels in the littoral zone of lakes (Miller 1941; Anderson and Hooper 1956; Okland 1964; Kajak and Rybak 1966; Efford 1967; Kajak and Dusoge 1971; Werner et al. 1977; Keast et al. 1978).

With the exception of Gerking (1962, 1972), studies on rates and efficiencies of energy transfer to freshwater fishes have been

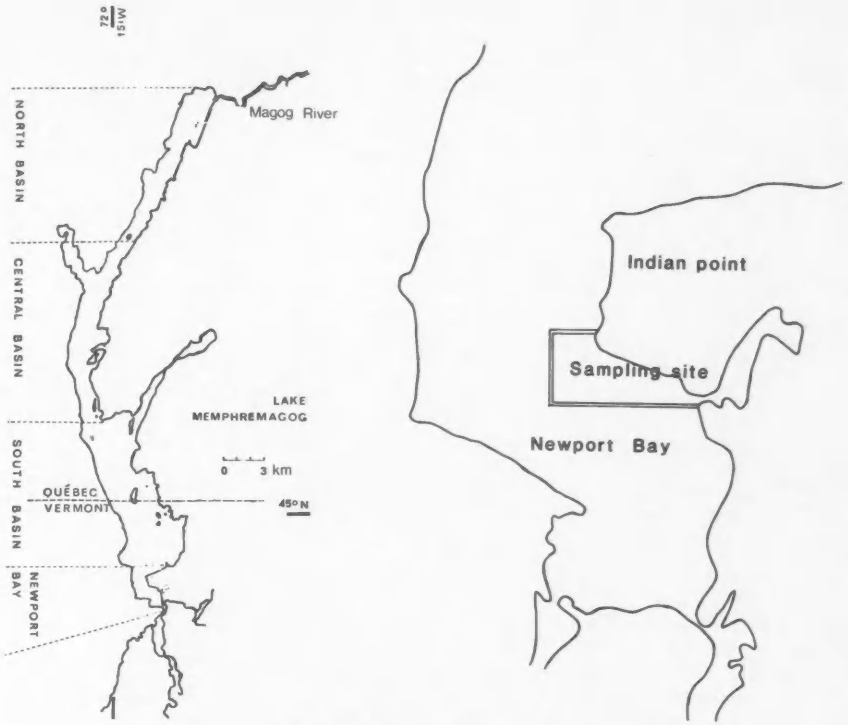

FIG. 1. Location of study area.

performed in rivers and streams (Allen 1951; Horton 1961; Mann 1964, 1965) and the littoral zone has been largely ignored. In this paper we report the results of a study designed to quantify the rate and efficiency of littoral zone food consumption by the total littoral zone fish community of a north-temperate lake.

Methods

The study was conducted in Newport Bay, a mesotrophic basin located at the southern tip of Lake Memphremagog (45°06′N; 72°17′W; Fig. 1) from May to September 1982. Detailed descriptions of the morphometry and water chemistry of Lake Memphremagog are given in Morse and Flanders (1971), Pagé (1971), Lands et al. (1974), and Ross and Kalff (1975).

Littoral Zone and Associated Biota

We defined the littoral zone as that area within which the light intensity at the bottom is at least 1% of the surface irradiance (Westlake et al. 1981). Unpublished data (J. Kalff, McGill University, pers. comm.) show that the 1% level of surface irradiance at Indian Point, adjacent to our study site (Fig. 1), occurs at 5.5–7.5 m in May, 4.5–6.5 m in June, and 3.5–5.5 m in July. Based on these data we identified the limit of the littoral zone as the 5-m isobath.

Our definition of the littoral zone biota potentially available to fishes as food (energy) was based on a preliminary analysis of what the fish actually ate and included plankton, macrophyte-associated invertebrates, benthic invertebrates, and forage fishes. Fishes <6 cm TL such as cyprinids were placed into both the predator and prey categories.

Fish Community Consumption in the Littoral Zone

Sampling

Fishes >6 cm TL were sampled with a 60 × 5 m knotless nylon standard seine (0.6-cm^2 mesh). The seine was deployed to fully enclose an area extending from the beach to the 5-m depth profile, and when hauled sampled a 700-m^2 area. By August 16 macrophyte growth had progressed to a point that made use of this seine ineffective. On this date a smaller 50 × 3 m knotless nylon bag seine was employed in a manner similar to the 60-m seine but extended only to the 3-m depth profile. When hauled it sampled an area of 460 m^2.

The capture efficiency of the 60-m seine was assessed by determining the recapture rate of marked fish introduced into the deployed seine. Twenty-five fish representing the three most abundant fish groups in the study area (rock bass, *Ambloplites rupestris*; pumpkinseed sunfish, *Lepomis gibbosus*; and yellow perch, *Perca flavescens* between 140 and 240 mm) were marked with fluorescent pigment (Phinney et al. 1967) and introduced into the seine on two occasions. The seine was hauled 10–15 min after their introduction and all fish captured were examined for marks under an ultraviolet lamp. Recapture rates were 24/25 and 25/25. Capture efficiency was therefore assumed to be 100%.

All fish in each sample were killed immediately after capture with an overdose of 2-phenoxyethanol. This successfully prevented regurgitation of stomach contents.

The total wet weight of fish (>6 cm TL) in predetermined size/species categories, hereafter referred to as "fish groups" (Table 1), was measured immediately after capture with an electronic balance accurate to 0.1 g. The complete digestive tract was removed within 4 h of capture from a maximum of 15

TABLE 1. Fish species and fish group designations used in text.

Species	Group name	Associated length class limits (mm) I	II	III
Ambloplites rupestris	Ambloplites	<140	140–240	>240
Catostomus commersonii	Catostomus	<140	140–240	>240
Esox niger	Esox	<250	250–500	>500
Etheostoma olmstedi	Etheostoma	<80	80–110	>110
Fundulus diaphanus	Fundulus	<80	80–110	>110
Hybognathus nuchalis	Hybognathus	<80	80–110	>110
Ictalurus nebulosus	Ictalurus	<140	140–240	>240
Lepomis gibbosus	Lepomis	<140	140–240	>240
Micropterus dolomieui	Micropterus do	<250	250–500	>500
Micropterus salmoides	Micropterus sa	<250	250–500	>500
Notemigonus crysoleucas	Notemigonus	<80	80–110	>110
Notropis atherinoides	Notropis at	<80	80–110	>110
Notropis volucellus	Notropis vo	<80	80–110	>110
Osmerus mordax	Osmerus	<140	140–240	>240
Perca flavescens	Perca	<140	140–240	>240
Pimephales notatus	Pimephales	<80	80–110	>110
Salmo gairdneri	Salmo	<250	250–500	>500
Stizostedion vitreum	Stizostedion	<250	250–500	>500

fish per group per sample. The contents of the total digestive tract of each fish group were pooled, weighed in the field to the nearest 0.01 g, and refrigerated. Dry weights of the pooled gut samples were determined within 3 d following drying at 60°C for 48 h. Dried gut contents were then stored in heat-sealed plastic bags.

Computations

In principal, total daily food consumption in the littoral zone could be estimated as the product of average fish biomass onshore and average daily ration. However, because of the large number of fish species involved, the possibility of significant between-species and size-related differences in daily ration and digestion rate (Ware 1975; Elliott and Persson 1978; Allen and Wootton 1982; Persson 1982, 1983), and diel variance in the biomass of individual fish groups onshore, we could not assume a priori that this averaging approach would yield unbiased estimates. We therefore calculated total daily food consumption as

$$D = \Sigma\, d_i \tag{1}$$

where D is the total daily food consumption (grams dry weight per square metre) on any sampling date and d_i is the daily food consumption (grams dry weight per square metre) of fish group i; d_i was calculated as

$$d_i = \sum_{\Delta=1}^{6} \bar{B}_{\Delta i} \cdot C_{\Delta i} \tag{2}$$

where $\bar{B}_{\Delta i}$ is the geometric mean biomass (grams wet weight per square metre) of fish group i during the time interval Δ and $C_{\Delta i}$ is partial daily ration (grams dry weight per 100 g wet weight) of fish group i during the time interval Δ; $\bar{B}_{\Delta i}$ was calculated as

$$\bar{B}_{\Delta i} = \exp\left\{\frac{[\ln(B_{(t+4)i}+1) + \ln(B_{ti}+1)]}{2}\right\} - 1 \tag{3}$$

where B is the biomass estimate (grams wet weight per square metre) of fish group i at time t and at $t + 4$ h; $C_{\Delta i}$ was calculated using the method of Elliott and Persson (1978):

$$C_{\Delta i} = \frac{(\bar{F}_{(t+4)i} - \bar{F}_{ti}\, e^{-R_i T}) R_i T}{(1 - e^{-R_i T})} \tag{4}$$

where $\bar{F}_{ti}$ and $\bar{F}_{(t+4)i}$ are, respectively, the mean gut fullness (grams dry weight per 100 g wet weight) of fish group i at the time of sequential diel sampling periods t and $t + 4$, R_i is the relative digestion rate (per hour) of fish group i, and T is the time interval between successive sampling = 4 h.

The mean gut fullness of fish group i at sampling time t was estimated as

$$\bar{F}_{ti} = \frac{\sum_{j=1}^{n} G_{ji}}{\sum_{j=1}^{n} W_{ji}} \times 100 \tag{5}$$

where G_{ji} is the dry weight (grams) of the digestive tract (stomach plus intestine) contents of fish j, group i, W_{ji} is the wet body weight (grams) of fish j, group i, and n is the number of fish analyzed for digestive tract contents in group i at sampling time t.

R_i is estimated as the slope of the relationship between digestion rate (r_i; grams dry weight per 100 g wet weight per hour) and mean gut fullness ($\bar{F}_{ti}$) of fish group i. Digestion rate is a positive linear function of gut fullness and passes through the origin (Elliott 1972). Hence, a single observation of the relationship between digestion rate and gut fullness allows the calculation of R_i. To equate rates of food disappearance to digestion rate, the assumption must be made that no consumption has occurred over the period considered. This assumption is most closely approximated immediately following a peak in the fullness index. Thus, the digestive rate r_i of fish group i was estimated as

$$r_i = \frac{\bar{F}_{(t+4)i} - \bar{F}^{*}_{ti}}{T} \tag{6}$$

where $\bar{F}^{*}_{ti}$ is the mean gut fullness of group i at the time of peak in gut fullness, $\bar{F}_{(t+4)i}$ is the mean gut fullness of group i at the subsequent sampling, and T is the time interval between successive samples = 4 h; R_i was in turn estimated as

$$(7) \quad R_i = \frac{r_i}{\bar{F}^*_{ti}}$$

where r_i is the digestion rate estimate of fish group i and $\bar{F}^*_{ti}$ is the value of mean gut fullness index of fish group i at a peak.

As an independent test of the reliability of the values of R_i derived by this method, we estimated R_i experimentally for the most common fish group, Perca II. Eighty specimens, collected by seining, were stocked into a 1-m^3 wading pool located at lakeside. A continuous flow of filtered lakewater was provided to the pool by pumping. Ten fish were sacrificed at the initiation of the experiment and an additional 10 were similarly sacrificed and examined each 4 h for 28 h. All sacrificed fish were dissected immediately and the dry weight of the complete digestive tract contents was determined as previously described.

Food Availability in the Littoral Zone

The biomass of littoral zone organisms potentially available as food was determined by quantitative sampling not more than 24 h prior to the initiation of fish sampling.

Five replicate samples of fishes <6 cm TL (considered to function as both predators and prey) were made with a 5.5 × 1 m knotless nylon bag seine (0.2-cm^2 mesh) which sampled a 30-m^2 area. Fishes <6 cm TL were pooled without reference to species and their total wet and dry weights were determined in the laboratory. Dry weights were determined following drying at 60°C for 48 h. No gut content analysis was performed on these fish.

Five replicate samples of benthos and plankton were collected at each of three stations located at the 1-, 3-, and 5-m depths along a transect running perpendicular to the shoreline. A different transect was used on each sampling date. Benthos was sampled with a 0.023-m^2 Eckman dredge. All organisms retained on a 0.250-mm-mesh seine were immersed in 70% ethanol for 15 min, transferred to 500 mosmol saltwater, and refrigerated. Dry weights were determined following drying at 60°C for 48 h. This method of preservation prevented significant changes in calorific content between sampling and analysis ($t_8 = 0.66$, $p > 0.05$).

Benthic organisms were the most abundant potential food source (95.9% of total biomass). Because depth distribution in the sediment and individual size are known to influence the availability of benthos as prey, we examined the distribution of benthos in the sediment column and the size of benthic organisms at the study site.

The vertical depth distribution of the benthos was determined from 15 sediment cores (17 cm long, 7 cm diameter) taken at the 3-m station on two dates during the season (July 23 and August 28). Cores were obtained using scuba and were refrigerated immediately after collection. All cores were sectioned in 1-cm slices within 3 h of collection. Eight core slices representing the top 8 cm of sediment were individually sieved through a 0.250-mm-mesh screen. Retained organisms were refrigerated until sorting, which was completed within 3 d of collection. The dry weight biomass of all organisms in each slice was determined to the nearest 0.01 g following drying for 48 h at 60°C.

Plankton was sampled via vertical net hauls obtained with a 0.5-m-diameter, 0.064-mm-mesh net. All plankton were killed by immersion in carbonated water and preserved in refrigerated 500 mosmol saltwater. Plankton dry weight was determined following filtration on 0.0012-mm glass fiber filters and drying for 24 h at 60°C.

The potential loss of invertebrate biomass from the system through emergence was evaluated by operating three 1-m^2 emergence traps during the 24-h fish sampling period. No emergence was detected. Invertebrates associated with macrophytes were sampled by hand removal of all plants from within a 0.10-m^2 quadrat at each station. The invertebrates sorted from the plants were added to the benthic invertebrate sample of the corresponding station.

Standardization of Food Availability

Comparison of the quantities of food consumed by the fish community foraging in the littoral zone with the quantities of food available there requires weighting the biomass of each food category to a standard surface area. Field observations and bathymetric maps indicated that each station was representative of one third of the littoral zone. Thus, equal importance was given to each station in the weighting process. The weighted biomass of a food type f during the sampling day s (W_{fs}) was estimated as

$$(8) \quad W_{fs} = \exp 1/3 \sum_{K=1}^{3} \ln \bar{B}_K$$

where $\bar{B}_K$ is the geometric mean biomass of food type f at station K ($K = 1$ represents 1 m depth; $K = 2$, 3 m depth; $K = 3$, 5 m depth) during sampling day s. This weighted biomass was calculated for all food types (Table 2) except fishes <6 cm for which the biomass estimate was used directly.

Energy Determination

Energy content (calories per gram dry total weight) was determined for digestive tract contents, and all potential food items (forage fish, benthic invertebrates, plankton, and macrophytes). The energy content of benthic invertebrates and digestive tract contents was measured directly with a Phillipson microbomb calorimeter. Energy values for forage fish, plankton, and macrophytes were obtained from Cummins and Wuycheck (1971).

There was a significant variability in the caloric values of digestive tract contents between fish groups ($F_{2,28} = 4.94$, $p < 0.01$). This was due exclusively to the effect of the gut contents of Lepomis II. The lower energy content per unit weight of the food of this group was due to the high proportion of pelecypods (*Sphaerium* spp.) in the diet. The dry weight/calorie conversion for Lepomis II was 2.046 $\mathrm{Cal \cdot g\ dry\ total^{-1}}$ (95% CI = 1.923–2.169); that for all other fish groups was 5.024 $\mathrm{Cal \cdot g\ dry\ total^{-1}}$ (95% CI = 4.714–5.334).

The mean dry weight/calorie conversion for benthic invertebrates over the sampling season was 2.878 $\mathrm{Cal \cdot g\ dry\ total^{-1}}$ (95% CI = 2.637–3.199). This low value relative to that for the gut content of fish groups other than Lepomis II is, again, due to the presence of significant numbers of pelecypods in the benthos samples.

The dry weight/calorie conversions employed for plankton, macrophytes, and forage fishes were 5.308, 3.402, and 5.086 $\mathrm{Cal \cdot g\ dry\ total\ weight^{-1}}$, respectively.

TABLE 2. Geometric mean food biomass by type and date: g dry·m^{-2}; (Cal·m^{-2}). Biomass values are weighted to an area of 1 m^2 representative of the three depth zones sampled.

	June 7	June 21	July 5	July 19	Aug. 1	Aug. 16
Plankton	—	0.86 (4.56)	0.26 (1.38)	1.77 (9.40)	0.52 (2.76)	1.57 (8.33)
Benthos	—	72.21 (207.82)	41.21 (118.60)	49.75 (143.18)	34.73 (99.95)	39.93 (114.92)
Fish	—	0.86 (4.37)	1.71 (8.70)	0.56 (2.85)	0.74 (3.76)	0.45 (2.29)

Results

Fish Biomass

A total of 18 fish species were sampled. These were assigned to 36 fish groups for analysis (Table 3). Perca I and II, Lepomis II, Ambloplites II, and Ictalurus III dominated the biomass (70% of the total). All other groups contributed less than 4% to the total biomass sampled (Table 3). Numerically, four fish groups (Perca I (22.9%), Hybognathus I (21.0%), Notemigonus I (15.2%), and Notropis vo I (13.2%)) dominated, comprising 72.3% of the total catch.

All species except rainbow trout (*Salmo gairdneri*, two specimens) and walleye (*Stizostedion vitreum*, three specimens) were common in the catch throughout the summer.

The average biomass of fish in the littoral zone was 10.80 g wet·m^{-2} (95% CI = 9.24–12.63). There was no significant diel or seasonal variability in the total biomass of fish sampled (ln transformed data; $F_{5,30} = 2.35$, $p > 0.05$ and $F_{6,30} = 1.70$, $p > 0.05$, respectively).

Relative Digestion Rate

The average group specific relative digestion rate (R_i) varied between 0.08 and 0.20·h^{-1} (Table 3). The mean R_i for the 27 fish groups for which this value could be calculated was 0.14 (95% CI = 0.13–0.15). At least five independent estimates of R_i were obtained for nine fish groups. There was no significant seasonal variation of R_i for these groups ($F_{4,32} = 0.52$, $p > 0.05$). R_i did, however, vary significantly between these nine groups ($F_{8,32} = 3.52$, $p < 0.01$). Significant differences between fish groups were also revealed when R_i values for all groups were compared taking sampling dates as replicates ($F_{26,83} = 1.89$, $p < 0.05$).

Gut fullness indices developed for fish sacrificed at each sampling period in the experiments designed to estimate R_i were plotted against time since first sampling (Fig. 2). The slope of the relationship ($\bar{x} = 0.072$; 95% CI = 0.054–0.090) did not differ significantly from field-derived estimates of R_i for Perca II ($\bar{x} = 0.10$; 95% CI = 0.05–0.15; $t_6 = 0.48$; $p > 0.05$).

Grove and Crawford (1980) have shown that R_i may differ significantly when calculated on whole gut versus foregut/stomach samples. Any future attempts to compare our R_i values with literature estimates should therefore be restricted to estimates based on whole gut analysis.

Daily Ration

The mean daily ration (grams dry weight per 100 g wet weight per day) for the 13 fish groups for which estimates could be obtained ranged from 1.15% to 3.92%. The grand mean of all individual estimates was 2.31% (95% CI = 1.89–2.73) (Table 3). There was no significant seasonal variation in daily ration in the four fish groups for which at least four estimates were calculated (Lepomis II; Notemigonus I; Perca II, III; $F_{3,11} = 1.19$; $p > 0.05$). There were, however, significant between-group differences when sampling dates were used as replicates ($F_{12,23} = 3.18$, $p < 0.01$).

The grand mean caloric daily ration was 9.64 Cal·100 g wet^{-1}·d^{-1} (range: 5.78 (Notemigonus II) to 18.73 (Notropis vo I)). This value differed significantly between fish groups ($F_{12,23} = 2.27$; $p < 0.05$).

Our estimates of daily ration for Perca II compare well with both theoretically and empirically derived estimates for perch of equivalent sizes. The basal metabolic rate (BMR) of fish is described by the equation (Winberg 1956)

$$(9) \qquad \text{BMR} = aW^b \text{ (watts)}$$

where W is the individual fish weight in kilograms. The exponent (b) normally assumes values between 0.70 and 0.80 (Peters 1983), whereas the intercept (a) typically ranges from 0.40 to 0.50 (Winberg 1956; Ware 1975). Daily energy expenditure is believed to range between 2.0 and 3.0 times the basal metabolic rate (Ware 1975; Kerr 1982), and assimilation coefficients typically range from 0.75 to 0.85 (Winberg 1956; Beamish 1972; Ware 1975; Elliott 1976a, 1976b). The surplus energy (Ware 1980, 1982) of Perca II in Lake Memphremagog was determined by Nakashima and Leggett (1975) to be 0.70 g wet·d^{-1} (0.15 g dry·d^{-1}; 0.77 Cal·d^{-1}). Using these values and the mean weight of Perca II (80 g) we derived daily ration estimates of 3.35–7.83 Cal·d^{-1}. These are consistent with our daily ration estimate for 80-g Perca II ($\bar{x} = 6.17$ Cal·d^{-1}; 95% CI = 3.13–9.22 Cal·d^{-1}).

Persson (1983) estimated that the daily ration of perch aged 2–3 yr, which correspond to our Perca II, ranged from 0.1 to 3.0 g dry·100 g wet^{-1}·d^{-1}. Energy equivalents calculated from food composition data provided by Persson were 0.54–16.0 Cal·100 g wet^{-1}·d^{-1}. Our estimates for Perca II were mean 1.54 g dry·100 g wet^{-1}·d^{-1} (95% CI = 0.78–2.30 g dry·100 g wet^{-1}·d^{-1} (3.92–11.56 Cal·100 g wet^{-1}·d^{-1}).

Food Consumption in the Littoral Zone

The total daily consumption of littoral zone food resources by the fish community foraging there averaged 0.30 g dry·m^{-2}·d^{-1} (ln transformed data; 95% CI = 0.20–0.44; Table 4), which corresponds to 1.27 Cal·m^{-2}·d^{-1} (ln transformed data; 95% CI = 0.87–1.85). The contribution of fishes <6 cm TL to these values (ln transformed data; $\bar{x} = 0.06$ g dry·m^{-2}·d^{-1}; 0.30

TABLE 3. Geometric mean biomass and relative contribution of each fish group to total catch, number of times one or two gut fullness peaks per day were observed, mean R, daily ration, and daily food consumption for each fish group sampled.

Fish group		Mean fish biomass		Peak·d^{-1}		$\bar{R}$	Mean ration	Mean food consumption
		g wet·m^{-2}	%	1	2	(h^{-1})	(g dry·100 g wet·$^{-1}$·d^{-1})	(g dry·100 m^{-2}·d^{-1})
Perca	II	3.02	32.45	0	6	0.10	1.54	3.78
Lepomis	II	1.85	19.89	4	2	0.11	3.92	6.96
Ambloplites	II	0.66	7.07	4	2	0.13	3.15	1.26
Perca	I	0.56	6.02	0	5	0.10	1.26	0.74
Ictalurus	III	0.40	4.32	5	0	0.14		0.74
Esox	II	0.36	3.82	1	1	0.20		1.15
Notemigonus	III	0.35	3.80	0	3	0.18		0.54
Perca	III	0.32	3.47	5	0	0.15		0.37
Notemigonus	I	0.29	3.07	0	5	0.20	2.41	0.71
Catostomus	II	0.22	2.39	2	0	0.10		0.46
Hybognathus	I	0.16	1.69	3	2	0.12	1.46	0.31
Ambloplites	III	0.16	1.68	1	0	0.12		
Notemigonus	II	0.15	1.60	4	0	0.16	1.15	0.22
Lepomis	I	0.11	1.22	5	0	0.15	1.64	0.28
Ictalurus	II	0.11	1.14	2	0	0.18		0.13
Esox	I	0.10	1.09	2	2	0.17	2.26	0.13
Hybognathus	II	0.07	0.79	3	0	0.08		0.13
Notropis vo	I	0.05	0.56	0	3	0.13	3.73	0.08
Micropterus do	II	0.04	0.46					
Etheostoma	I	0.04	0.40	2	3	0.17	2.03	0.09
Esox	III	0.04	0.39					
Micropterus sa	I	0.03	0.37	0	4	0.17		0.02
Fundulus	I	0.03	0.36	2	3	0.12	1.37	0.06
Ambloplites	I	0.03	0.36	4	2	0.17		0.02
Notropis at	II	0.03	0.32			0.10		
Catostomus	I	0.03	0.28	4	0	0.12	2.84	0.05
Pimephales	I	0.03	0.28	5	0	0.08		0.01
Catostomus	III	0.02	0.22					
Salmo	II	0.01	0.15					
Stizostedion	II	0.01	0.12					
Notropis at	I	0.01	0.08	1	0	0.20		0.01
Ictalurus	I	0.01	0.05	1	0	0.12		
Micropterus do	I	0.01	0.05					
Lepomis	III	0.01	0.05					
Stizostedion	I	<0.01	0.02					
Osmerus	I	<0.01	<0.01	2	0			

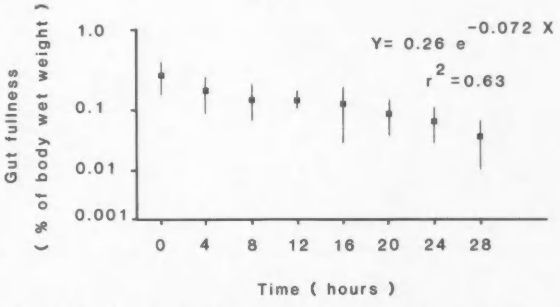

FIG. 2. Food evacuation from the whole gut (stomach plus intestine) of fish group Perca II during starvation. Vertical lines represent 95% CI.

Cal·m^{-2}·d^{-1}) was estimated by assuming that their ration was equivalent to the average daily ration of all fish groups sampled (2.31 g dry·100 g wet^{-1}·d^{-1}). The average daily consumption estimates for individual fish groups are presented in Table 3.

Food in the Littoral Zone

The mean biomass of fishes <6 cm TL potentially available as prey to larger fishes was 0.77 g dry·m^{-2} (95% CI = 0.61–0.98; Table 2). Differences between sampling dates were significant (ln transformed data; $F_{4,20} = 11.71$, $p < 0.001$).

The mean biomass of benthic invertebrates in the littoral zone was 45.98 g dry·m^{-2} (95% CI = 36.96–57.18). No significant difference in mean biomass occurred between sampling dates (ln transformed data; $F_{4,68} = 1.57$, $p > 0.05$). Significant biomass differences were, however, detected between depths (ln transformed data; $F_{2,68} = 6.49$, $p < 0.01$); the mean benthic biomass at 5 m was significantly less than that at 1 and 3 m. No difference in mean biomass was evident between the 1- and 3-m sites (Duncan's multiple range test; $p < 0.05$). The mean benthic biomass at our study site was higher than estimates for 46 North American lakes and ponds (0.1–34.2 g dry·m^{-2}; Hanson and Leggett 1982). This difference may result from the high densities of pelecypods in our samples. The contribution of this non-nutrient material to total biomass estimates under-

TABLE 4. Daily food consumption by the littoral zone fish community, total littoral zone food biomass, and food biomass corrected for benthic invertebrate availability and food exploitation rate (%).

	June 7	June 21	July 5	July 19	Aug. 1	Aug. 16
Fish community consumption						
g dry·m^{-2}	0.54	0.21	0.37	0.29	0.28	0.21
Cal·m^{-2}	(2.07)	(0.89)	(1.67)	(1.35)	(1.24)	(0.81)
Total food biomass						
g dry·m^{-2}	—	73.93	43.18	52.08	35.99	41.95
Cal·m^{-2}	—	(216.75)	(128.68)	(155.43)	(106.47)	(125.54)
Available biomass						
g dry·m^{-2}	—	50.82	29.99	36.16	24.88	29.17
Cal·m^{-2}	—	(150.25)	(90.73)	(109.61)	(74.49)	(88.77)
Food exploitation rate						
% of total food biomass	—	0.28	0.86	0.56	0.78	0.50
% of total calories	—	(0.41)	(1.30)	(0.87)	(1.16)	(0.65)
% of available biomass	—	0.41	1.23	0.80	1.13	0.72
% of available calories	—	(0.59)	(1.84)	(1.23)	(1.66)	(0.91)

lines the importance of energy units in comparisons of food availability between sites.

The dry weight biomass of benthos varied significantly with depth in the sediments (ln + 1 transformed data; July $F_{7,112} = 11.26$, $p < 0.001$; August $F_{7,112} = 6.62$; $p < 0.001$). Only those benthic invertebrates occurring in 1 cm of sediment were considered available (Nikolski 1963). The biomass of invertebrates in the 0–1 cm strata ranged from 86% (July) to 63% (August) of the total in the 0–8 cm depth zone. These values did not differ significantly (Wilcoxon two samples test, $p > 0.05$) and combined gave a value of 68% (arithmetic mean).

The prey handling capability of fish is known to be determined by gape (Keast and Webb 1966). Numerous authors have reported that the maximum width of prey animals consumed corresponds closely to the mouth width of the predator (Northcote 1954; Lawrence 1958; Yasuda 1960; Okada and Taniguchi 1971; Wong and Ward 1972; Wankowski 1979). Burko (1975) found that the handling time for prey >0.8 times the mouth width increased six- to seven-fold. We therefore adopted 0.8 times the gape width as the upper limit of the available benthos size fraction. The mouth gape of 26 specimens belonging to the three main benthivorous fish groups (Ambloplites II, Lepomis II, Perca II), measured using the method of Keast and Webb (1966), ranged from 1.2 to 3.8 cm ($\bar{x} = 2.08$; 95% CI = 1.82–2.34). The maximum width of benthic invertebrates found in the top 1 cm of sediments ranged from 0.22 to 2.15 cm ($\bar{x} = 0.70$; 95% CI = 0.61–0.79). We therefore considered 100% of the benthos in this depth zone to be available to the suite of fish predators foraging in the littoral zone. Available benthic biomass (B_A) was determined by

$$(10) \quad B_A = B_e \cdot P_1$$

where B_e is the benthos biomass estimate (Table 2) and p_1 is the proportion of benthos biomass sampled by the Eckman dredge that lies within the surface first centimetre.

Weighted benthic biomass estimates (Table 2) were thus multiplied by 0.68 to correct for availability before summation of available biomass estimates of all food types (Table 4).

The mean plankton biomass (0.79 g dry·m^{-2}; 95% CI = 0.59–1.08) was comparable with values provided by Matuszek (1978) for 12 North American lakes (range: 0.15–1.65 g dry·m^{-2}). Plankton biomass showed significant seasonal (ln transformed data; $F_{4,68} = 8.99$, $p < 0.001$) and depth (ln transformed data; $F_{2,68} = 8.35$, $p < 0.001$) variation.

Food Exploitation Rate in the Littoral Zone

The rate of food exploitation in the littoral zone by fishes was calculated by dividing the food consumed by the food biomass in the littoral zone. This calculation was made in two ways: one using total food biomass and one total food biomass corrected for benthos availability (Table 4).

The mean daily rate of exploitation of the *total* food biomass was 0.55% by weight. The mean caloric rate was 0.81%. The mean rate of exploitation of the *available* food biomass was 0.80% (dry weight) and 1.15% (caloric).

Assuming an annual feeding period of 130 d, the littoral zone biomass/energy necessary to support these exploitation rates on an annual basis was estimated to be 72% of the mean summer *total* biomass (dry weight) and 105% of the mean summer *total* caloric standing crop. These rates equate to 104% of the average *available* biomass (dry weight) and 150% of the average *available* energy.

Our estimate of a 130-d feeding period is based, in part, on data in Keast (1968) that indicate that feeding of the rock bass, the pumpkinseed sunfish, and the yellow perch, the major components of the total fish biomass in our study, begins in the spring when temperatures average approximately 9°C. The annual duration of temperatures >9°C in Lake Memphremagog is approximately 160 d (Nakashima and Leggett 1975; J. Kalff, unpubl. data). However, Keast (1968) also found that food consumption in nine north-temperate fish species, including the yellow perch, the rock bass, and the pumpkinseed sunfish, increases three- to four-fold as temperature increases from 8 to 15°C in the spring. This is consistent with observations on seasonal variability in daily ration (Nakashima and Leggett

TABLE 5. Geometric mean littoral zone food exploitation rates (%) derived from an error analysis (1000 iterations) and from field sampling ($n = 5$). Also shown are 95% confidence intervals based on $n = 1000$ and on 5 rate estimates drawn at random from the population of 1000 generated rate estimates.

	Exploitation rate		95% confidence interval	
	$n = 1000$	$n = 5$	$n = 1000$	$n = 5$
% of *total* food standing crop consumed				
Daily				
Dry weight	0.58	0.55	0.56–0.60	0.32–0.95
Caloric	0.88	0.81	0.85–0.90	0.47–1.40
Annual				
Dry weight	75.22	72.13	73.15–77.34	41.30–126.59
Caloric	113.55	105.36	109.32–116.79	59.80–185.63
% of *available* food standing crop consumed				
Daily				
Dry weight	0.95	0.80	0.92–0.99	0.35–1.81
Caloric	1.44	1.15	1.38–1.50	0.51–2.61
Annual				
Dry weight	123.72	104.0	118.77–128.88	45.97–235.27
Caloric	187.12	150.0	179.59–194.96	66.30–340.93

1978; Allen and Wootton 1982). Nakashima and Leggett (1975) also reported that in Lake Memphremagog, perch growth occurred over a period of approximately 100 d. We therefore assumed an intermediate annual feeding period of 130 d and assumed further that the average feeding rates we observed apply over this interval.

Error Analysis

We calculated approximate 95% confidence limits for daily consumption rates by simulation. In this analysis the values of the input parameters used to calculate daily exploitation rates were drawn at random, following a normal distribution, from within the upper and lower 95% confidence interval of the ln normalized data. There were two exceptions to this procedure: first, the distribution of F values was normal and hence no transformation was necessary; second, the distribution of values of the coefficient of availability could not be normalized by standard transformations. We therefore divided the observed distribution into five equal classes. During the iterative process, each class was selected in proportion to its frequency, and individual values from within the class were then chosen at random assuming a uniform distribution. Estimates of the annual exploitation rate were generated in a similar fashion with the addition that the length of the feeding season was allowed to vary between 100 and 160 d assuming a normal distribution with a mean of 130 d.

One thousand daily and annual estimates of the *total* and *available* food exploitation rate (dry weight and caloric) were generated by iteration.

These data indicate that, given the error in our input parameter estimates, daily exploitation rates should vary between 0.32 and 0.95% of the total food biomass and between 0.35 and 1.81% of what we have defined as available food biomass. Corresponding caloric rates are 0.47–1.40% and 0.51–2.61% (Table 5).

Discussion

This is the first study in which community exploitation rates have been estimated for fishes foraging in the littoral zone of lakes. It is also the first study in which estimates of fish community consumption were estimated directly through an analysis of feeding rates and biomass for individual species and size groups, previous studies having estimated rates of consumption from growth data using physiologically based models. The latter approach, first applied to fish in Allen's (1951) study of Horokiwi Stream, yielded estimates of consumption ranging from 40 to 150 times the mean annual invertebrate biomass. This implies a production/biomass (P/B) ratio ranging from 40 to 150 if the invertebrate population is to sustain the predation imposed by brown trout (*Salmo trutta*) in the system. Gerking (1962) argued that Allen's estimates were 2–3 times too large because he applied adult growth efficiency values (Pentelow 1939) to the total population. More reasonable estimates would thus lie in the range 13–75 times the mean annual biomass. Horton (1961) estimated the exploitation rate of the brown trout in Dartmoor Stream to range from 8.7 to 26.0 times the mean annual food biomass. Using data in Mann (1964) we calculated the consumption rates of roach and bleak in the River Thames to be 18.7 times the mean annual food biomass if fish not directly sampled (Mann 1965) were excluded from the analysis and 47.4 times the mean annual food biomass when these fish were included. We similarly used data from Gerking (1962, 1972) to calculate the annual exploitation rate of the population of bluegill sunfish (*Lepomis macrochirus*) in Lake Wyland. Our estimates ranged from 1.7 times the mean annual biomass when the food supply was equated to the July biomass to 8.1 times the mean annual biomass when the August biomass was used.

The annual exploitation rates we derived for Lake Memphremagog (95% CI = 0.41–1.3 times the mean summer biomass dry weight) are much lower than those reported for lotic environments. This is not unexpected, since lotic systems are typically more productive than lentic systems (Wetzel 1975; Hynes 1979).

Taking a broader view of the relationship between food availability and rates of consumption, several workers have assumed (Lindeman 1942; Ivlev 1945; Slobodkin 1960; Sheldon et al. 1977) that for systems in equilibrium, consumption should approximate production of food items. This suggests that predator community exploitation rates should approximate the P/B ratio in the prey community.

This prediction is not supported by available P/B estimates. We estimated the mean daily P/B ratio (corrected for mortality) for three diptera species in the south basin of Lake Memphremagog to be 0.02 using data in Dermott et al.(1977). The P/B ratio corresponding to our estimates of community exploitation rate ($\bar{x}$ = 0.01) are significantly lower than Dermott et al.'s ($t_8 = 2.38$; $p < 0.05$). Data in Banse and Mosher (1980) indicate that the annual dry weight P/B ratio for different taxa of benthic invertebrates in 20 temperate lakes averages 3.11. The P/B ratio corresponding to our estimates of annual dry weight exploitation rate ($\bar{x}$ = 1.04) is significantly smaller than these values ($t_{23} = 2.34$; $p < 0.05$).

The factor or factors preventing higher exploitation rates by individual fishes or by the total fish community in the short term are presently unknown. Given the low daily and seasonal rates determined here, the potential for such short-term gain appears substantial.

One possibility is that foraging rates of individual fish are constrained by the energetic cost/benefit equation relating to foraging. For example, Brocksen and Bugge (1974), Elliott (1976a, 1976b), and Caulton (1978) have shown that assimilation efficiency is inversely proportional to daily ration. Moreover, growth efficiency in fish is known to decrease with daily ration (Paloheimo and Dickie 1966). Hence, the marginal energetic value of each prey item declines as ration increases. Feeding rates could therefore be limited by the interaction between the per item energetic cost of feeding and the marginal energetic value of the prey. Empirical support for this hypothesis is found in Ware's (1975) analysis of Ivlev's (1960) study of bleak (*Alburnus alburnus*). In this planktivorous species the interaction function describing net food intake and cost of foraging as a function of swimming speed (foraging cost) defined an optimal swimming speed ($111\ \mathrm{m \cdot h^{-1}}$) beyond which both growth and growth efficiency declined monotonically. This effect of foraging cost on the marginal value of prey organisms provides a possible mechanism by which exploitation rates of individual fish may be limited. This could explain the low exploitation rates observed in the short term. It again fails, however, to deal with the question of why fish numbers/biomass would not increase in the medium term to more fully exploit the apparent surplus of available biomass.

A second hypothesis, and one that we favour, is that the low community exploitation rates observed result from the difference between *potential* and *real* food availability. Benthic organisms were the dominant prey of the fishes we studied. In our analysis we assumed that 68% of the total benthos biomass (i.e. that located in the top 1 cm) was available. It is well known, however, that few fish systematically mine the benthos for prey. Hence, while a significant fraction of the prey items in the top 1 cm are *potentially* available as prey, a much smaller proportion are likely to be visible, and hence *truly* available, at any given time. Moreover, only a fraction of those prey at or on the surface of the sediment will be pursued by fishes. This fraction will depend on the interacting effects of fish density, reactive distance (Ware 1971; Werner and Hall 1974), prey colour (Ginetz and Larkin 1973), fish preference (Sutterlin and Sutterlin 1970; Sutterlin 1975), prey contrast (Ware 1975; English 1983), and apparent prey size (O'Brien et al.1976). Basic probability theory would predict that the *available* biomass should increase as a positive linear function of *total* biomass. This would explain the positive linear response of fish yield and biomass to total benthic biomass (Matuszek 1978; Hanson and Leggett 1982).

A better quantitative definition of availability, and of the contribution of habitat differences to its variance, are badly needed. Such knowledge would contribute both to the understanding of mechanisms regulating fish production and biomass in lakes, and to the accuracy of their prediction from empirical models.

If daily exploitation rate is an accurate measure of food availability, our data indicate that the ratio of available to total food biomass in the littoral zone will approximate 1%. This can be expected to vary between habitats due to differences in substrate type, macrophyte density, species composition of the predator and prey communities, etc. The strength of the empirical relationships between benthic invertebrate biomass and fish biomass and yield, in spite of acknowledged difficulty in obtaining accurate individual estimates of these parameters, suggests, however, that this ratio will vary within relatively narrow limits.

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Factors Regulating in situ Filtering Rates of Cladocera

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Individual filtering rates of four species of *Daphnia*, as well as *Holopedium*, *Diaphanosoma*, *Ceriodaphnia*, and *Bosmina*, were measured in 10 lakes under various field conditions to identify important factors regulating in situ filter-feeding for these cladocerans. Linear regression analysis indicated that carapace length accounted for almost 60% of the total variance in individual filtering rates when data from all 10 lakes were pooled. We suggest that zooplankton in these lakes filter-feed in proportion to their volume, since the functional slope of this regression approximated 3. Taxonomic affiliation had generally little effect on filtering rates. Temperature, ranging from 12 to 22°C, had no statistically significant effect on filtering rate; there were also no significant differences between rates measured at dawn and dusk compared with midday rates for animals ranging in size between 0.30 and 1.30 mm. Addition of phytoplankton concentration as a second independent variable to the regression relating filtering rate to length further increased explained variance to 64%. Since the two main determinants of in situ filtering rates were zooplankton carapace length and concentration of edible phytoplankton, both of which are independent of taxonomic affiliation, investigators interested in assessing grazing losses should seriously consider measuring zooplankton in terms of size distribution rather than taxonomic affiliation.

On a quantifié, dans diverses conditions, les taux de filtration individuels chez quatre espèces de *Daphnia* et chez *Holopedium*, *Diaphanosoma*, *Ceriodaphnia* et *Bosmina* peuplant 10 lacs, afin de déterminer les principaux facteurs qui règlent la filtration *in situ* de ces cladocères. Selon une analyse de régression linéaire, la longueur de la carapace expliquait presque 60 % de la variance totale des taux de filtration individuels quand les données recueillies dans les 10 lacs étaient groupées. Les auteurs formulent l'hypothèse que ce zooplancton lacustre se nourrit par filtration en fonction de son volume, car la pente fonctionnelle de cette régression se rapprochait de 3. Les liens taxonomiques avaient généralement peu d'incidence sur les taux de filtration. La température, qui variait de 12 à 22°C, n'avait aucun effet statistiquement significatif sur ce taux ; de plus, il n'y avait aucune différence significative entre les taux quantifiés à l'aube et au crépuscule par rapport à ceux qui étaient mesurés à midi chez les animaux dont la taille variait de 0,30 à 1,30 mm. L'ajout de la concentration du phytoplancton (comme seconde variable indépendante de la régression établissant un rapport entre le taux de filtration et la longueur) a fait passer la variance expliquée à 64 %. Comme les deux principaux facteurs déterminants des taux de filtration *in situ* étaient la longueur de la carapace du zooplancton et la concentration de phytoplancton comestible, deux facteurs indépendants des liens taxonomiques, les chercheurs qui s'intéressent à l'évaluation des pertes par broutage devraient sérieusement contempler la quantification de la taille du zooplancton au lieu des liens taxonomiques.

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Cladoceran zooplankton grazing imposes a basic loss on phytoplankton in pelagic ecosystems, and considerable effort has been channelled towards quantifying this loss (Gliwicz 1969, 1970; Porter 1972; Cushing 1976; Thompson et al. 1982). These attempts, however, have been hampered by an incomplete understanding of factors regulating filter-feeding in the field. Although many laboratory studies have been conducted they have limited predictive value for natural situations, because they are generally single-variate experiments involving at most a few zooplankton and phytoplankton species (McMahon and Rigler 1965; Burns 1969; Ivanova 1969; Buikema 1973; Geller 1975; Lampert 1977), or multivariate experiments that have been necessarily limited to varying two variables at a few discrete levels (Schindler 1968; Hayward and Gallup 1976). There is a limit to the extent that laboratory studies can ever mimic lake conditions. Thus, while laboratory studies are useful in elucidating basic physiological mechanisms, field data must ultimately be used to evaluate the importance of factors regulating filter-feeding in natural populations. Our objective was to utilize field measurements of individual zooplankton filtering rates under natural conditions in a range of lakes to evaluate the relative importance of laboratory-identified factors in determining in situ filter-feeding activity.

In previous studies, filtering rates of *Daphnia* sp. have been found to vary as a function of simple morphological parameters

TABLE 1. Description of lakes in study area.

Lake	Township	Surface area (km^2)	Volume (Mm^3)	$\bar{Z}$ (m)	Z_{max} (m)	pH
Gull	Lutterworth	9.96	164.34	16.50	49.10	7.5
Moore	Lutterworth	1.83	13.80	7.56	21.60	6.0
Hall's	Stanhope	5.40	150.66	27.90	79.20	6.0
St. Nora	Stanhope	0.33	5.32	16.00	40.00	6.0
Head	Laxton/Digby	9.18	32.13	3.50	8.30	7.5
Mountain[a]	Minden	3.19	44.12	13.43	31.39	6.5
Plastic	Sherborne	0.33	2.64	8.10	16.76	5.6
Brady	Hindon	0.89	4.08	4.56	11.58	5.8
Blue Chalk	Ridout	0.50	4.70	9.37	21.95	6.0
Picard	Cavendish	0.76	7.69	10.15	35.05	7.4

[a] Measurements include A and B basins.

such as body weight (Richman 1958) and body length (McMahon 1965; Burns 1969). They were also found to be a function of biophysical parameters such as temperature (Burns 1969; Chisolm et al. 1975; Geller 1975), light (McMahon 1965; Buikema 1973) edible phytoplankton concentration (McMahon 1965; Geller 1975; Kersting and van der Leeuw 1976), and time of day in which rates were measured (Haney and Hall 1975; Starkweather 1975, 1983; Duval and Geen 1976). Blue-green filaments were also found to have inhibitory effects on feeding rates (Burns 1968; Webster and Peters 1978; Porter and Orcutt 1980; Gliwicz and Siedlar 1980). In this study, we examine the effect of some of these factors on in situ filtering rates. By evaluating the importance of these parameters, we are able to build an empirical model to predict filtering rates for a number of cladoceran species, and thereby free investigators of having to perform tedious and time-consuming grazing experiments in the field.

Materials and Methods

The 10 study lakes are in south central Ontario and vary considerably with respect to lake morphometry (Table 1). Mountain Lake has two distinct basins (A and B) that were sampled separately and treated as two water bodies. Total phosphorus in these lakes ranged from 5 to 12 $mg \cdot m^{-3}$, Chl *a* ranged from 0.8 to 4.0 $mg \cdot m^{-3}$, and pH ranged from 5.6 to 7.5.

Brady, Mountain A and B, Plastic, and Picard lakes were sampled in 1981; the remaining lakes were sampled in 1982. Each lake was visited once between June and September except for Mountain B and Plastic lakes, which were visited twice during the summer of 1981. Lakes were sampled at one station, usually at the deepest part of the basin.

We followed the procedure outlined in Holtby and Knoechel (1981) for labelling algae with ^{14}C. The algal species used were *Chlorella vulgaris* (6–8 μm, longest dimension) and *Scenedesmus ovalis* (4–6 μm; Indiana Culture Collection) in 1981 and 1982, respectively. Sufficient radioactive cells to bring the specific activity in the grazing chamber to at least 1000 $cpm \cdot mL^{-1}$ were added. Final concentration of labelled algae in grazing chambers ranged from 1000 to 5000 $cells \cdot mL^{-1}$. This addition constitutes less than 10% of natural phytoplankton biomass in each lake.

Grazing Experiments

All of the grazing experiments were performed in situ using a 2-L Haney (1971) chamber, because filtering rates were depressed when animals were first concentrated by vertical hauls with a plankton net and then placed into experimental beakers (P. Chow-Fraser, unpubl. data). Feeding experiments were conducted at various depths throughout the water column and the ambient water temperature corresponding to each experiment was monitored. Experiments were all conducted between 10:00 and 16:00, except for two sets of experiments comparing midday grazing rates with those measured at dawn (06:00) and at dusk (20:00).

Animals were allowed to feed at the depth of sampling for 10 or 15 min and were then collected on 64-μm-nitex screen. They were subsequently killed with hot water, rinsed with at least 1 L of filtered lakewater, and then stored frozen on dry ice until they were sorted. Replicate 5-mL aliquots of the labelled grazing-chamber water were also collected to determine available food radioactivity.

Edible Phytoplankton Concentration

Phytoplankton samples were collected to determine edible phytoplankton concentration in water strata corresponding to the depths at which grazing experiments were conducted. Integrated samples from 0–4 and from 4–8 m were collected with a tube sampler. The sampler consisted of two lengths of tygon tubing (inside diameter 1.5 cm) joined by a tubing connector. The upper portion was 4.5 m long, the lower 4.0 m; iron weights were attached to the lower end of the sampler. The apparatus was lowered slowly at right angles to the water surface. Water level inside the tubing was visually monitored during the descent to ensure that there was no more than a few centimetres difference between inside and outside water levels. Once 8 m of tubing had been submerged, the upper end was clamped shut and the lower end was retrieved by means of an attached string. In this manner, an 8-m column of water was obtained. The column was then split by carefully disconnecting the tubing connector, and the upper and lower portions were separately retained. After the procedure was repeated, upper and lower portions were respectively combined and subsamples were preserved with Lugol's iodine solution.

Samples from the 4-m column corresponding to the depths at which most of the grazing data were collected were then analyzed. Algal biomass was estimated from calculations of algal biovolumes. Phytoplankton freshweight (milligrams) was estimated to be equal to the calculated biovolumes on the basis that cell contents have a specific gravity of 1. Cell volumes were approximated by assigning simple geometric shapes to cells and using average cell dimensions in volume formulae. The edible portion of the phytoplankton was operationally defined as algae whose maximum linear dimension were $<30\ \mu m$.

Animals, stored in petri plates on dry ice, were sorted without addition of water or preservative. Zooplankton were identified using a dissecting microscope. *Daphnia* spp. were measured from the base of the tailspine to the anterior-most point of the carapace along the long axis of the body. Length of the body, excluding spines and setae, was measured for the remaining genera. For convenience, all of the length measurements will be referred to as "carapace length." Animals were stored individually in scintillation vials before they were prepared for scintillation counting.

Radioactivities of the available algae of replicate 5-mL samples of grazing-chamber (GC) water were determined by liquid scintillation counting in Aquasol II counting solution. Animals were individually digested in scintillation vials overnight at 50°C with 0.25 mL of NCS tissue solubilizer (Amersham). Radioactivities of the zooplankton were determined by liquid scintillation counting in OCS counting solution (Amersham; recommended for use with NCS). The procedure for scintillation counting for both algae and zooplankton is given in Holtby and Knoechel (1981). Zooplankton filtering rates were calculated as

$$\underset{(\mathrm{mL\cdot animal\cdot d^{-1}})}{\text{Filtering rate}} = \frac{\text{dpm in animal}}{\text{dpm in 1 mL GC water}} \times \frac{1440\ \mathrm{min\cdot^{-1}}}{\text{time spent in GC}}.$$

Statistical Analyses

A predictive slope is used to make predictions of y on x whereas a functional slope is a "measure of the central trend of a natural distribution" (Ricker 1973). For example, the predictive regression is appropriate for making predictions of filtering rate for animals sampled in study lakes and is not appropriate for cross-study comparisons. The functional slope, on the other hand, is appropriate for determining whether the power function of the relationship between filtering rate and length is 2, 3, or an intermediate value and is appropriate for cross-study comparisons. Under certain experimental conditions the predictive regression is a good estimate of the functional regression; however, when distributions of the data are open-ended and non-normal (see Table 2) the functional regression should be used routinely both for description and prediction (Ricker 1973). In past studies, investigators have tended to use the predictive regression indiscriminantly to estimate both functional and predictive slopes. Consequently, most reported values are actually estimates of the predictive regression, although they have been interpreted as functional regressions. To keep our values comparable with those in literature, we report both functional as well as predictive slopes, recognizing that predictive slopes from different studies should be compared cautiously.

Predictive regressions were estimated using Model I least-squares regression analyses (Ray 1982); functional regressions were estimated by Model II regression analyses (geometric mean regression) because both carapace length and filtering rate were subject to a combination of inherent variability and measurement error (Ricker 1973). At present, the standard error of the slope from a geometric mean regression is estimated by the standard error of the slope from Model I regression. Model I least-squares regression analyses were also used to compute a multiple linear regression equation of filtering rate as a function of both carapace length and edible phytoplankton concentration, and to compare regression equations after the data were sorted by lake and species.

TABLE 2. Summary of normality tests, using Kolmogorov–Smirnov D-statistic (SAS; Ray 1982). Values of $P < 0.05$ denote significant departure from normality (FR = filtering rate; L = length; $n = 845$).

Variable	D	P
FR	0.2104	<0.01
$\log_{10}$ FR	0.0893	<0.01
L	0.0864	<0.01
$\log_{10} L$	0.1175	<0.01

To test differences among zooplankton species with respect to filtering rates, we selected data obtained at approximately the same time, at the same depth, and within the same lake so that effects of temperature and diet composition were held constant. This procedure eliminated all but three lakes for the comparison. Small sample sizes for two lakes also necessitated a graphical rather than statistical analysis.

To determine if the high variance noted for small animals (*Bosmina*) was due to biological variability or due to Poisson variability in particle-encounter frequencies inherent in the experimental procedure, we investigated the effect of encounter rate of tracer cells on the variability of filtering rate. To test whether or not *Bosmina* ingested tracer cells randomly during the grazing period, a chi-square test of variance-to-mean ratio (Elliott 1979) was used.

Data distributions were tested for significant departures from normality with the Kolmogorov–Smirnov D-statistic for sample size >50, and with the Shapiro–Wilk W-statistic for sample size <51 (Ray 1982). Variance-ratio test was used to test for homogeneity of variance (Zar 1984). We tested differences between midday rates and those measured at dawn and at dusk, and the effect of temperature on filtering rate in St. George Lake using two-way analysis of variance (Ray 1982). A nonparametric two-factor analysis of variance (Ray 1982) was used to test the effect of temperature on filtering rate in Plastic Lake because data distributions did not have homogeneous variances.

Results and Discussion

Our pooled dataset comprises 845 individual filtering rates measured in 10 lakes of different trophy over the course of two summer seasons. No attempt was made to regulate the percent contribution of any species to the dataset. In total, eight cladoceran species were sampled. Of the four *Daphnia* species identified, the dominant ones in the study were *D. galeata* ($n = 189$) and *D. dubia* ($n = 63$); *D. rosea* ($n = 35$) and *D. pulex* ($n = 21$) were present in only a few experiments. *Holopedium* ($n = 190$) and *Bosmina* sp. ($n = 251$) were collected mainly from Plastic Lake, although some measurements on these species were obtained in most of the other lakes. *Diaphanosoma* ($n = 12$) was present but rare in 6 of the 10 lakes. *Ceriodaphnia* ($n = 33$) was a dominant zooplankter in Head Lake and was seldom present in other study lakes. Fifty-one daphniids could not be identified and remained in the analysis as *Daphnia* sp. Experi-

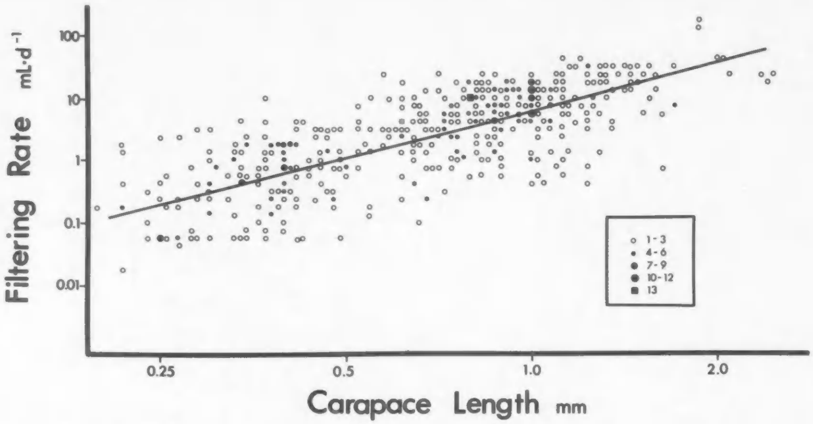

FIG. 1. Filtering rate vs. carapace length for data pooled from all lakes ($n = 845$). Solid line represents Model I least-squares regression (see Eq. 1). Each number corresponding to a symbol in the box represents number of overlapping points.

TABLE 3. Comparison of functions relating filtering rate to zooplankton body length (FR = $mL \cdot d^{-1}$).

Investigator	Zooplankton species	Relationship
McMahon 1965	*D. magna*	$\log_{10} FR = 2.20 \log_{10} L + 0.83$
Burns 1966	*D. rosea*	$\log_{10} FR = 3.02 \log_{10} L + 0.87$
Geller 1975	*D. pulex*	$\log_{10} FR = 2.42 \log_{10} L + 0.88$
DeMott 1982	*D. rosea*	$\log_{10} FR = 2.41 \log_{10} L + 0.81$

mental temperatures ranged between 10 and 22°C; in most cases, however, they were above 18°C.

Carapace Length

With the exception of a semi-log relationship reported by Hayward and Gallup (1976), filtering rate and zooplankton body length have generally been related in a log–log fashion (Table 3). Therefore, we first present a plot of filtering rate versus carapace length for the pooled data to examine the generality of the relationship.

A striking feature of the relationship between filtering rate and carapace length is the extreme variability in filtering rates (Fig. 1). Considering the heterogeneous composition of our dataset, however, this variability is not surprising. Since our measurements are of individual rates rather than group means, variability is probably due in large part to individual variability of ingestion rates. Narita and Ward (1972) found that filtering rates for an average 2.0-mm *D. similis* ranged from 1.3 to $32.3 \, mL \cdot d^{-1}$, with a mean of $20.8 \, mL \cdot d^{-1}$, despite the fact that their experiments were conducted under laboratory-controlled conditions. Thompson et al. (1982) also showed a 10-fold range in filtering rate of similar-sized animals in the field. There was high variation within a single grazing experiment. Replicate experiments at the same depth yielded equally variable results compared with data from experiments performed at the same temperature in different lakes (Table 4). The high coefficients of variation observed in Table 4 suggest that individual variation contributed substantially to overall variation in the pooled data. Besides individual variation, however, some variability may be associated with the insensitivity of the method to accurately measure individual rates of small animals such as *Bosmina*.

TABLE 4. Basic descriptive statistic of grazing data corresponding to single experiments, all conducted at 20–22°C. Only *D. galeata* (1–1.5 mm) are included in this analysis.

Lake	Depth (m)	*n*	Uncoded mean	Coefficient of variation (%)
Brady	4	3	5.75	46.44
Gull	4	6	13.96	27.41
Head	1	17	3.91	109.59
	2	6	1.04	1929.60
	3	5	1.51	302.11
	3	6	3.01	106.36
Moore	5	3	11.75	45.28
Mountain B	2	10	1.85	85.74
	3	8	6.16	17.21
	3	4	3.41	30.52
	4	16	3.95	77.41
	4	6	3.40	69.66
	5	6	8.32	10.48
	5	22	1.40	439.97
	7.5	6	3.37	105.31

Variation in encounter rates of food particles becomes random when the amount of water filtered and hence number of particles ingested are low ($<1.0 \, mL \cdot d^{-1}$; <5 cells·animal^{-1}). Because the ingestion rate of tracer cells for *Bosmina* is extremely low (rarely more than 15 cells during a grazing period), we speculate that the great individual variability in *Bosmina* filtering rate is due to random encounter probabilities. A chi-square test of variance-to-mean ratio for agreement with a Poisson distribution (Elliott 1979) indicates that *Bosmina* does in fact ingest tracer cells at random (Table 5). When ingestion rates are random, reliability of individual rates are severely reduced. Therefore, much of the variability associated with filtering rates of *Bosmina* is artifactual rather than natural. In order to increase reliability, we would have to greatly increase the encounter rate; however, since encounter rate cannot be further increased without altering the algal concentration in the

TABLE 5. Chi-square test of variance-mean ratio for agreement with a Poisson distribution (Elliott 1979) to determine if *Bosmina* sp. ingested tracer cells randomly. Values of $P > 0.05$ denote conformity with randomness.

Mean no. of cells ingested per grazing period	s^2	df	χ^2	P
1.66	0.45	9	2.43	>0.97
4.00	2.16	18	36.72	>0.25
7.51	4.58	27	35.23	>0.25
14.48	17.14	24	28.41	>0.25
16.33	16.65	23	23.45	>0.25
20.15	18.15	37	33.32	>0.25

grazing chamber, it seems impractical to assay individual variation in these animals using the Haney method.

Despite the large variability, carapace length was nevertheless an important predictor of filtering rate for the pooled dataset. A least-squares regression analysis produced a significant log–log relationship between filtering rate (FR; millilitres per day) and carapace length (*L*; millimetres) (*F*-test; $P = 0.0001$), accounting for almost 60% of the variability in filtering rate ($r^2 = 0.589$):

(1) $\log \mathrm{FR} = 2.45\ (\pm 0.071) \log L + 0.80\ (\pm 0.020)$

(numbers in parentheses are standard errors). The slope of the regression is equivalent to the exponent when filtering rate is expressed as a power function of body length. Our exponent of 2.45 compares well with those previously described in laboratory studies (Table 3) in which *Daphnia* filtering rate has been described as a function ranging between a square and a cube of zooplankton body length.

We employed Model II (geometric mean) regression to generate a functional slope for the pooled data, producing the following regression equation:

(2) $\log \mathrm{FR} = 3.19 \log L + 0.93.$

Whereas slope of the predictive equation more nearly approximates a square of length, slope of the functional equation exceeds a cubic function of length. This comparison points out the inappropriateness in most cases of using the predictive slope to estimate the functional slope when both variables are subject to natural variability and measurement error. Only in cases where variance is very high (i.e. Blue Chalk and Hall's lakes in Table 6) does the predictive slope approximate the functional slope. The difference between the mean Model I slope of 2.45 and the mean Model II slope of 3.19 is not merely academic, because the value of the exponent indicates that animals in our lakes generally filter-feed in proportion to their volume rather than to surface area. However, this functional slope might be biased by lakes with large sample size, and might not be representative of all study lakes. This possible bias was examined by reorganizing the pooled data to yield regressions for individual lakes.

Functional slopes of the sorted data, representing the 11 water bodies, range from 2.67 to 3.95, the majority lying between 2.85 and 3.40 (Table 6). Mean value for these slopes, 3.22, is very similar to 3.19, slope of the pooled regression. Comparison of these regression coefficients (Tukey–Kramer method, Sokal and Rohlf 1981) indicates that they are statistically homogeneous ($P > 0.05$). Therefore, functional slopes for these lakes appear to approximate 3. Predictive slopes of the lake-specific regressions are also statistically homogeneous ($P > 0.05$); the mean value, 2.49, is again very similar to exponent value of the pooled regression, 2.45.

Statistical homogeneity in slopes for both these models indicates that the exponent in the filtering rate – length relationship is consistent from lake to lake despite the heterogeneous nature of the data. Mixed zooplankton assemblage, temperatures ranging from 10 to 22°C, and mixed phytoplankton communities all appear to have minimal effects on the exponent value. Since published observations indicate that zooplankton species (Burns 1969; Table 3), temperature (Burns 1969; Chisolm et al. 1975), and time of day (Starkweather 1983) can affect the exponent, a more detailed assessment of effects of these factors on filtering rates was conducted.

Zooplankton Species

A visual comparison of data corresponding to various cladoceran species in Brady and Mountain A lakes (Fig. 2) indicates that filtering rates are scattered about the regression line without any obvious pattern of species. Therefore, although no statistical comparisons can be made, these distributions do not appear to support the observation made by Burns (1969) that exponents associated with various *Daphnia* species are different.

The larger sample size of Head Lake facilitated a statistical comparison of filtering rates corresponding to *Ceriodaphnia*, *D. galeata*, and *D. dubia*. Linear regression analyses indicate that slope of the regression equation corresponding to *Ceriodaphnia* is significantly different from those of the two *Daphnia* species ($P = 0.0336$), although differences between *Daphnia* species are not statistically significant ($P = 0.3306$). Filtering rates associated with *Ceriodaphnia* are consistently higher than those of similar-sized *Daphnia* (Fig. 3). Although this comparison confirms observations made by Neill (1975) and Lynch (1978) that adult *Ceriodaphnia* are more efficient filterers than juvenile *Daphnia*, L. B. Holtby (unpubl. data) found that *Ceriodaphia* did not consistently filter more efficiently than daphniids. The data again do not support observations made by Burns (1969) that different species of *Daphnia* require different regression equations.

DeMott (1982) reported differences between slopes for *Daphnia* and *Bosmina*, showing that filtering rate of *Daphnia* increased as a cube of length whereas that of *Bosmina* increased only as a square. In our study the data are too variable to resolve possible differences in regressions for the zooplankton species; the predictive and functional slopes corresponding to two species of *Daphnia* and *Bosmina* were homogeneous (Table 7) ($P > 0.05$). In all cases, the predictive slope approximated 2, whereas the functional slope approximated 3.

We also assessed the effect of zooplankton species on filtering rate by comparing lake-by-lake distributions of *D. galeata*. Filtering rates of *D. galeata* corresponding to seven study lakes are plotted together in Fig. 4 to illustrate the large intraspecies variation that existed across lakes. This large variation is in fact as great in magnitude as the interspecies variation in Head Lake (Fig. 3). Additionally, a comparison of lake-by-lake regressions reveals that the slopes are all homogeneous ($P = 0.9893$). Functional slope of the combined data is 3.07, compared with the predictive slope of 2.43. This disparity between functional and predictive slopes is again very similar to that for the pooled data described earlier.

Temperature

Filtering rates (corresponding to animals ranging from 0.30

TABLE 6. Regression statistics of filtering rate (mL·d^{-1}) on carapace length (mm) for each lake; *P* represents the probability of obtaining observed slope if the true value is zero as determined by an *F*-test.

Lake	*n*	Regression model	Slope	SE	Intercept	SE	r^2	*P*
Brady	17	I	2.69	0.531	0.90	0.162	0.632	0.0001
		II	3.39		1.04			
Moore	24	I	3.15	0.507	0.98	0.193	0.638	0.0001
		II	3.95		1.19			
Picard	33	I	2.25	0.453	0.99	0.049	0.444	0.0001
		II	3.38		0.91			
Gull	17	I	2.14	0.410	0.99	0.044	0.640	0.0001
		II	2.67		1.00			
Mountain A	23	I	2.33	0.422	0.98	0.092	0.592	0.0001
		II	3.03		1.01			
Plastic	390	I	2.72	0.106	0.96	0.034	0.633	0.0001
		II	3.42		1.13			
Hall's	7	I	3.15	0.318	0.95	0.060	0.952	0.0002
		II	3.22		0.95			
Mountain B	170	I	2.15	0.173	0.62	0.039	0.481	0.0001
		II	3.11		0.72			
Head	121	I	2.52	0.220	0.68	0.069	0.523	0.0001
		II	3.48		0.88			
St. Nora	13	I	1.67	0.692	0.41	0.148	0.347	0.0342
		II	2.84		0.49			
Blue Chalk	24	I	2.60	0.389	0.48	0.095	0.818	0.0001
		II	2.88		0.44			

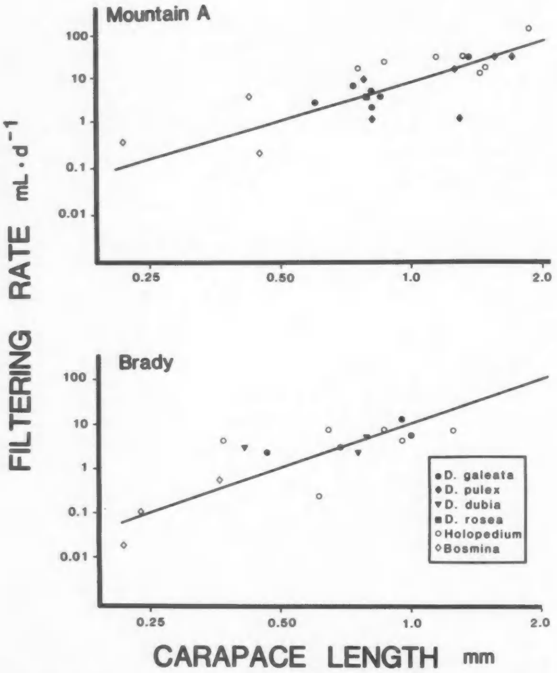

FIG. 2. Filtering rate vs. carapace length for Mountain A and Brady lakes. Solid lines indicate Model I least-squares regression through data.

to 1.20 mm) from Plastic Lake were grouped into five length intervals so that effect of temperature could be tested using two-way analysis of variance (Table 8). We found no statistically significant effect of temperature on filtering rates in the range of 10–20°C. Absence of a significant effect was not likely due to inclusion of many species in the analysis, since taxonomic affiliation did not appear to have had a noticeable effect on filtering rates in other lakes with this species-mix. Table 8 also included two analyses using single-species data from St. George Lake. (L. B. Holtby, unpubl. data). Data were grouped into appropriate length intervals and the effect of temperature was also tested using two-way analysis of variance. Again, we found no significant effect of temperature on filtering rates.

Haney (1973), Haney and Hall (1975), and Downing and Peters (1980) also failed to find a relationship between filtering rate and temperature in the field. By contrast, the effects of temperature on filtering rates in laboratory experiments have been somewhat varied. Whereas some investigators reported no significant effect (Schindler 1968; Buckingham 1978; Armitage and Lei 1979), others have reported a general trend towards higher filtering rate with increasing temperatures, although they do not concur on slope of the curve nor on optimum temperature (McMahon and Rigler 1965; Burns 1969; Kibby 1971; Geller 1975; Chisolm et al. 1975; Hayward and Gallup 1976; Kersting and van der Leeuw 1976). Armitage and Lei (1979) and Kibby (1971) have alluded to the possible role of temperature acclimatization in regulating filter-feeding in the field. Nonacclimatized animals apparently show little or no temperature effects. Kibby showed that within a range from 12 to 20°C, temperature optimum for filtering rate can be entirely a function

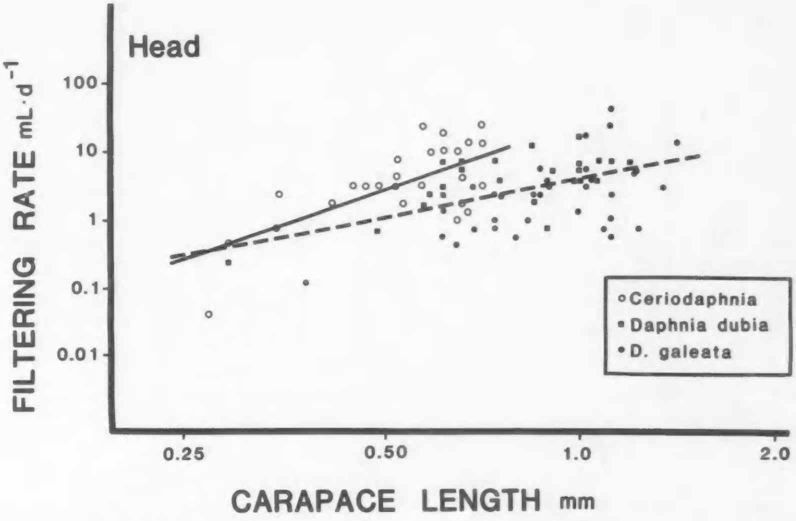

FIG. 3. Filtering rate vs. carapace length. Solid line represents Model I least-squares regression through *Ceriodaphnia* data; broken line represents regression through *Daphnia* data. Slopes of regressions corresponding to the two *Daphnia* species were homogeneous ($P = 0.3306$).

TABLE 7. Comparison of regression statistics of filtering rate ($mL \cdot d^{-1}$) on carapace length (mm) for *Bosmina* and *Daphnia* spp.; *P* represents the probability of obtaining observed slope if the true value is zero.

Zooplankton species	*n*	Regression model	Slope	SE	r^2	*P*
D. galeata[a]	56	I	2.32	0.235	0.644	0.0001
		II	2.89			
D. pulex	35	I	2.00	0.435	0.390	0.0001
		II	3.20			
B. longirostris	18[b]	I	2.16	0.525	0.513	0.0008
		II	3.01			

[a] Excluding data from Head, Mountain B, St. Nora, and Blue Chalk lakes. These lakes have significantly lower intercepts than other lakes in study.

[b] These represent means of animals grouped into 0.1-mm length intervals.

of the temperature at which animals are grown. In the current study, grazing experiments were conducted in situ at the depth and temperature of collection. Lack of a significant temperature effect might thus be interpreted as an indication that zooplankton under natural conditions are not acclimatized to a specific temperature.

Time of Day

Two sets of experiments were conducted to test the effect of time of day on filtering rate in Plastic and Mountain B lakes. Filtering rates were compared from experiments conducted at dawn (06:00) and at midday (13:00) in Plastic Lake and data from experiments conducted at dusk (20:00) and midday (14:00) in Mountain B Lake (Table 9). Results of the two-way analysis of variance indicate no significant diel differences in filtering rate for either *D. galeata* or *Bosmina* in our study. These results contrast findings of several field investigators who found increased rates at dawn and dusk compared with midday rates (Nauwerck 1959; Haney and Hall 1975; Duval and Geen 1976), and several laboratory experiments that have also indicated higher nighttime filtering rates (Starkweather 1975, 1983; Chisolm et al. 1975; Peterson et al. 1978). One reason for lack of a consistent effect in our study may be the relatively small size of animals in our samples (0.3–1.2 mm). Starkweather (1983) and Haney and Hall (1975) found that the largest size-classes generally underwent the greatest amplitude of daily change in feeding, while the smallest animals changed very little over the same period. However, Thompson et al. (1982) and L. B. Holtby (unpubl. data) found no nighttime increase in their field experiments that included large animals. Effect of time of day on field-measured filtering rates is obviously inconsistent and the reasons for this should receive further investigation.

Results of the preceding analyses indicate that zooplankton species, temperature, and time of day had no significant effect on filtering rates in our lakes, and therefore, these factors probably had no effect on the exponent of the functional relationship between filtering rate and carapace length. On the other hand, the intercepts vary considerably, from 0.44 to 1.19

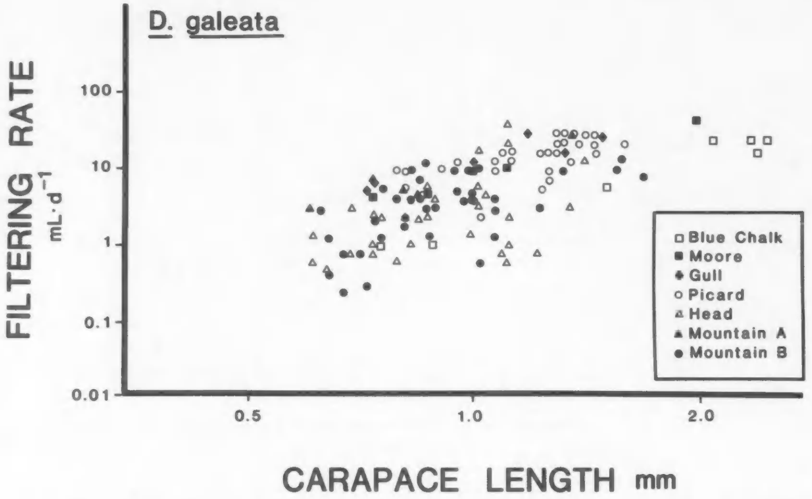

FIG. 4. Filtering rate vs. carapace length for *D. galeata*. Data were pooled from seven study lakes.

TABLE 8. Summary of two-way ANOVA's comparing cladoceran filtering rates at various temperatures. Values of $P < 0.05$ indicate a significant effect.

Temperatures tested (°C)	Lake	Experimental animal	*n*	Source of variation	*P*
10, 13, 20	Plastic	Cladocerans[a]	114	Temperature	0.9545
		(0.30–1.20 mm)		Carapace length	0.0001
				Temperature × length	0.8331
12, 17	St. George	*Daphnia pulex*[b]	94	Temperature	0.9374
		(1.0–3.0 mm)		Carapace length	0.0001
				Temperature × length	0.7118
17, 22	St. George	*Daphnia galeata*[b]	36	Temperature	0.2117
		(0.80–1.60 mm)		Carapace length	0.0001
				Temperature × length	0.7867

[a] Include *Holopedium*, *Daphnia* spp., and *Bosmina* spp.

[b] L. B. Holtby (unpubl. data).

(Table 6). Since the antilog of the intercept is equivalent to the predicted filtering rate of a 1-mm animal, the intercepts thus provide a means of comparing filtering-rate performance between lakes where regression slopes are similar. Although regression of intercepts on edible phytoplankton concentration was not significant ($P = 0.4860$), we added edible phytoplankton concentration to the general regression model because filtering rate has been found to vary inversely with food concentration beginning at a critical level referred to as the incipient limiting level (ILL) (McMahon and Rigler 1965).

Addition of edible phytoplankton concentration to the Model I regression increased the r^2 value from 0.589 to 0.636 ($P = 0.0001$) and yielded the following equation:

$$(3)\quad \log \mathrm{FR} = 2.74\ (\pm 0.084) \log L - 0.63\ (\pm 0.206) \log \mathrm{ED} + 2.30\ (\pm 0.454).$$

The negative value of the regression coefficient reflects the possible inhibitory effect of edible phytoplankton concentration on in situ filtering rate even at the low levels encountered in our lakes. Since the edible phytoplankton concentrations in the study lakes ranged from 40 to 400 mg·m^{-3}, the negative coefficient suggests that ILL in these lakes is lower than most published ILL values (Table 10). McMahon (1965) and Downing and Peters (1980) have suggested that ILL varies as a function of grazer body size. Since most animals in this study were small (1.2 mm) relative to those reported in Table 10, our lower ILL value may simply reflect the smaller zooplankton in our lakes. Another possible reason for this difference is that animals in laboratory experiments grazed on unialgal cultures, whereas animals in our lakes grazed on phytoplankton of diverse species and sizes in combination with detritus and inorganic particulate matter. Our data therefore indicate that the relationship between algal concentration and filtering rate in nature cannot be extrapolated from laboratory studies alone, since in situ filtering rate was detectably affected by phytoplankton concentration at levels lower than those examined in previous studies.

Empirical Model of Filter-Feeding

Carapace length emerged as the most important predictor of in situ filtering rate in our study. Together with edible phytoplankton concentration, it explained 64% of the variation in filtering rate (Eq. 3). Since this two-variable model was empirically derived from data that included *Daphnia* spp.,

TABLE 9. Summary of ANOVA's comparing diel differences in cladoceran filtering rates. Values of $P < 0.05$ indicate a significant effect.

Time of day tested	Lake	Experimental animal	n	Source of variation	P
Dusk and day (20:00 and 14:00)	Mountain B	*Daphnia galeata* (0.70–1.20 mm)	30	Time of day Carapace length Time × length	0.3771 0.0126 0.8204
Dawn and day (06:00 and 13:00)	Plastic	*Bosmina longirostris* (0.20–0.50 mm)	58	Time of day Carapace length Time × length	0.4580 0.0488 0.7025

TABLE 10. Summary of published incipient limiting level (ILL) values.

Investigators	Zooplankton species	Food species	ILL	
			$\text{cells} \cdot \text{mL}^{-1}$	$\text{g} \cdot \text{m}^{-3}$
McMahon and Rigler 1965	*D. magna* (2.8–3.3 mm)	*Chlorella*	2.5×10^5	5[a]
Porter et al. 1982	*D. magna* (2.7 mm)	*Chlamydomonas*	1.0×10^4	1.5[b]
Chisolm et al. 1975	Arctic *Daphnia* (2.3–2.6 mm)	*Chlamydomonas*	2.6×10^4	11.0[c]
Geller 1975	*D. pulex* (2.0 mm)	*Scenedesmus*	0.9×10^4 – 4.5×10^4[d]	1–5
Hayward and Gallup 1976	*D. schoedleri* (1.5–2.0 mm)	*Chlamydomonas*	3×10^4	4.1–12.3[c]
Burns and Rigler 1967	*D. rosea* (1.6 mm)	*Rhodotorula*	2.5×10^4	0.5[e]

[a] Extrapolated from fig. 1B (McMahon and Rigler 1965) and assuming a biovolume of 20 μm^3 for *Chlorella* (Nalewajko 1966).

[b] Calculated from the reported dry weight value of $0.54\ \text{g} \cdot \text{m}^{-3}$ and assuming that dry weight is 36.0% of the biovolume for *Chlamydomonas* (Nalewajko 1966).

[c] Using Nalewajko's (1966) biovolume for *Chlamydomonas* of 410 μm^3.

[d] Calculated on the basis that each cell has a biovolume of 111 μm^3.

[e] Assuming a biovolume of 20 μm^3 (using published dimensions).

Holopedium, *Bosmina*, *Diaphanosoma*, and *Ceriodaphnia* that were collected under environmentally diverse conditions, it should be generally applicable. However, the model does not apply to calanoid copepod species (P. Chow-Fraser, unpubl. data; Chow-Fraser and Wong 1985) nor does it apply to lakes in which blue-green algal filaments are prevalent (P. Chow-Fraser, unpubl. data). Lakes ranging from oligotrophy to mesotrophy in which the species-mix is similar to that found in our lakes should be good candidates for testing the applicability of this model.

This empirical model for cladoceran filter-feeding will be particularly useful for generating large-scale estimates of community grazing rates in situations where grazing data are not available, or cannot be easily obtained. Since accurate sampling is a prerequisite to realistic models of energy transfer between phytoplankton and zooplankton, we hope that this model will permit investigators to concentrate on more accurate sampling rather than on sample processing.

Differences in nutritional status of animals could have contributed to the large individual variation associated with the relationship between filtering rate and length, since starvation can drastically influence the biomass–length relationship for some cladocerans (Berg 1936; Tessier et al. 1983; Holtby 1981). Therefore, future studies should consider biomass as another useful determinant of filtering rate. Diel differences in field-measured filtering rates for large versus small animals should be given attention. Interference from inedible algal forms as well as usefulness of other "edibility" criteria in the model also need to be examined.

Our results indicate that filtering rates do not vary systematically among cladoceran species. Length alone was a good determinant of filtering rate. Different cladoceran species appear to respond to changing lake conditions homogeneously, and thus treatment of zooplankton based on size rather than on taxon would seem justified. Investigators interested in assessing the impact of losses on the phytoplankton should recognize that species data without corresponding length measurements are not appropriate for calculating grazing losses.

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Early Life History of Atlantic Mackerel (*Scomber scombrus*) in the Southern Gulf of St. Lawrence

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Ware, D. M., and T. C. Lambert. 1985. Early life history of Atlantic mackerel (*Scomber scombrus*) in the southern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. 42: 577–592.

Results of a 4-yr study of the vertical distribution, development, and mortality of the early life history stages of Atlantic mackerel (*Scomber scombrus*) in St. Georges Bay, Nova Scotia, are summarized. Adult mackerel migrate to the southern Gulf of St. Lawrence and first appear in St. Georges Bay in the spring when the sea surface temperature is 7–8°C. Peak spawning occurs about 26 d later, when the water temperature has warmed to 13°C. Mackerel eggs tend to concentrate near the surface, particularly under light winds, and decline exponentially with depth. The rate of decline was a function of egg diameter and the temperature gradient in the top 5 m. During incubation, which lasts about 6 d, the median depth of the eggs increased at a rate of 1 m/d. This explains why recently hatched larvae were primarily between 5 and 10 m. As the larvae grew they moved progressively closer to the surface during the day; between the 3- to 8-mm stage the median depth decreased at a rate of 0.7 m/d. Mortality in the egg stage was of the order of 41%/d, and increased with respect to the annual rate of warming of the mixed layer. Larval mortality rates (corrected for net avoidance) were about 42%/d and were positively correlated with temperature. Although the mortality rate tended to be higher amongst first-feeding larvae, events during this stage did not change the rank order of abundance of the year classes — mortality was consistently high from fertilization to the 8-mm stage. There is some evidence in 1975, which was the warmest year, and the year with the highest larval mortality rate, that there was a poor spatial match between the size of mackerel larvae, at different depths, and the size of their planktonic food supply.

Le présent rapport résume les résultats d'une étude de 4 ans de la distribution verticale, du développement et de la mortalité des premiers stades vitaux du maquereau bleu (*Scomber scombrus*) peuplant la baie St. Georges (Nouvelle-Écosse). Les adultes migrent vers le sud du golfe du Saint-Laurent et font leur première apparition dans cette baie au printemps, quand la température superficielle de l'eau est de 7–8°C. La fraie atteint son apogée plusieurs 26 jours plus tard quand l'eau a atteint 13°C. Les œufs ont tendance à se concentrer près de la surface, surtout quand le vent est léger, et leur nombre diminue exponentiellement en fonction de la profondeur. Le taux de diminution est fonction du diamètre de l'œuf et du gradient de température dans les 5 premiers mètres. Pendant l'incubation, qui dure environ 6 jours, la profondeur médiane des œufs a augmenté à un taux de 1 m/jour. Ceci explique pourquoi les larves récemment écloses sont surtout présentes entre 5 et 10 m. La croissance des larves était accompagnée d'un déplacement progressif vers la surface pendant de jour ; lorsque l'animal mesurait entre 3 et 8 mm, la profondeur médiane a baissé à un taux de 0,7 m/jour. Chez les œufs, la mortalité se chiffrait à 41 % par jour et augmentait en fonction du taux annuel de réchauffement de la couche mixte. Les taux de mortalité des larves (corrigés pour l'action d'éviter le filet) s'élevaient à environ 42 % par jour et étaient en corrélation positive avec la température. Le taux de mortalité avait tendance à être plus élevé chez les larves nouvellement devenues nageuses, mais les événements pendant ce stade n'ont pas changé le classement par ordre de grandeur de l'abondance des classes d'âge ; la mortalité était uniformément élevée à partir de la fertilisation jusqu'au stade de 8 mm. Certains faits portent à croire qu'en 1975, année la plus chaude, où le taux de mortalité des larves a été le plus élevé, la coïncidence spatiale entre la taille des larves à différentes profondeurs et la taille du plancton-proie était faible.

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Atlantic mackerel (*Scomber scombrus*) is an active, pelagic species which completes a complicated annual spawning and feeding migration in the Northwest Atlantic. The schools are abundant in Canadian coastal waters from June to October. In autumn, they migrate offshore to overwintering areas along the edge of the Continental Shelf from Sable Island to Long Island. Sette (1950) was the first to discover that the Northwest Atlantic stock has two components. Elements of the southern component move inshore from mid-March to mid-April between Cape Hatteras and Delaware Bay. In mid-April to mid-May they migrate northward and spawn until June between New Jersey and Long Island; in summer they can be found feeding in the coastal waters of the

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Gulf of Maine. Schools belonging to the northern component move shoreward from the Continental Shelf off New England and southern Nova Scotia in the spring, and migrate northeastward along the Nova Scotia coast. Most of the northern component enters the southern Gulf of St. Lawrence and spawns from early June to mid-August. After spawning, the schools disperse to feed in the southern gulf and off the Newfoundland coast, temperatures permitting.

Most of what is known about the early life history of Atlantic mackerel has been summarized by Sette (1943). He traced the fortunes of the 1932 year class of the southern component to test Hjort's critical period hypothesis, and found that mortality during the early developmental stages was not sharply higher for first-feeding larvae — it was substantial in all stages, averaging between 10 and 14% of the cohort per day. The subsequent failure of the year class was attributed to a general scarcity of plankton, and to an abnormal drift pattern that transported the larvae further than usual from their nursery ground.

Recently, recruitment (at age 1) to the stock has varied by a factor of 18 — from 428 million fish in the 1962 and 1963 year classes to 7791 million fish in the 1967 year class (Anderson and Paciorkowski 1980, table 16). Although Sette (1943) recognized that these variations are caused by fluctuations in the abundance of the spawning stock, and in the mortality rate of the young stages, the operative process was, and still is, problematical. The purpose of our study, therefore, was to identify some of the biological and environmental factors affecting reproduction, growth, and mortality of the early life history stages of Atlantic mackerel in the southern Gulf of St. Lawrence. Although it is impossible to draw unconditional conclusions with only a few years of data, our results show that the mortality rate was uniformly high during the incubation and early larval stages, and was positively correlated with the rate of warming and water temperature. There is some indication that these correlations may reflect the fact that the spatial distribution of food, and possibly predators, changes with temperature.

Survey Design and Methods

Extensive plankton sampling was carried out in St. Georges Bay, Nova Scotia, from 1973 to 1976 inclusive. The data for 1978 came from neuston samples collected by Gareth Harding, Marine Ecology Laboratory. A brief account of the survey design and sample processing methods follows; a more detailed description is given by Lambert et al. (1982).

Stations were occupied at approximately weekly intervals from early June to early September. The investigation in 1973 was largely exploratory, so samples were taken only at the surface and 10 m at arbitrary stations throughout the Bay. In subsequent years, stations were fixed after being chosen randomly from a grid (Fig. 1). The number of stations was reduced in 1975 and 1976 as a cost-saving measure.

Neuston samples were collected with a box-type frame (Sameoto and Jaroszynski 1969). The other horizontal samples were collected at 5 m (1974, 1976) and at 10 m (1974, 1975, 1976) with 0.5-m-diameter ring nets (except in 1973 when an Isaacs–Kidd midwater trawl was fished at 10 m). All nets were towed simultaneously over a distance of 1 nautical mile at a speed of 4 knots. At the end of each station a bathythermograph was cast, followed by a vertical plankton haul. The mesh size of all nets was 405 μm, except for the vertical haul which was 80 μm. All net samples were collected during the day, except in 1976 when sampling was conducted at night.

The preserved samples were seived in the laboratory to improve the recovery of mackerel eggs and larvae, and to determine the size composition of the plankton. Each sample was washed through a stack of screens with mesh size (top to bottom) of 1050, 860, 602, and 405 μm and in the case of vertical samples, an additional two screens: 253 and 80 μm. The plankton on each screen was weighed and then sorted visually for fish eggs and larvae, except for the 80-μm-net fractions from the vertical haul, which were only weighed because they contained few fish eggs and larvae. All ichthyoplankton were identified, counted, and measured (note that the lengths given in this paper are standard lengths, unless otherwise specified). Wherever possible the entire sample was examined; if this was not practical, it was weighed and then reduced with a plankton splitter for sorting.

The methods used to estimate the mean age, the temperature-dependent duration, probability of capture, and the total production of each developmental stage are outlined in Appendices A and B. Larval production estimates were not attempted in 1973 because of difficulties in estimating the volume filtered by the midwater trawl. However, a crude estimate of egg production was obtained for 1973 by extrapolating from surface concentrations using the relationship between depth and abundance derived from the 1974–76 data (see Eq. 1, vertical distribution section).

Later we refer to a number of "seasonally weighted means" which were calculated for different variables, such as water temperature and zooplankton size. This expression indicates that the observed value of the variable, in each sampling period, was weighted by the estimated production rate of a specified developmental stage of mackerel in the same period. For example, if on three separate occassions during the production season, 4-mm larvae are being produced at a rate of 150, 200, and 50/d, and the corresponding temperature at the median depth the larvae inhabit is 12, 15, and 18°C, respectively, the unweighted mean temperature would be 15°C, whereas the weighted mean is 14.3°C. Since the latter statistic was obtained by weighting the temperature in each sampling period by the production rate, it more accurately represents the average temperature experienced, in this example, by the 4-mm stage.

Before discussing the early life history of Atlantic mackerel, it seems appropriate to digress briefly at this point to consider the main physical features of the study area. Much of the physical oceanographic data has been summarized by Drinkwater (1978) and Petrie and Drinkwater (1978).

Physical Oceanography

St. Georges Bay has a surface area of 1160 km^2 at low water and a mean depth of 28 m. In May the water temperature decreases almost linearly with depth, from 4°C at surface to 0°C near bottom. Typically, by the beginning of July a 10-m surface mixed layer of 14–15°C has developed and the bottom temperature has warmed by 1 or 2°. Peak surface temperatures of 20°C occur in August when the mixed layer is 20–25 m thick; bottom temperatures are then 5–10°C. After mid-August the mixed layer begins to cool — stratification has broken down by early November and isothermal conditions of 10°C prevail.

Salinity stratification is small throughout the year with maximum differences between surface and bottom waters of 1–2‰. Surface salinities are about 29‰ throughout the spring and decrease slightly below 28.5‰ in late August.

From June to October the mean flow in the mixed layer moves

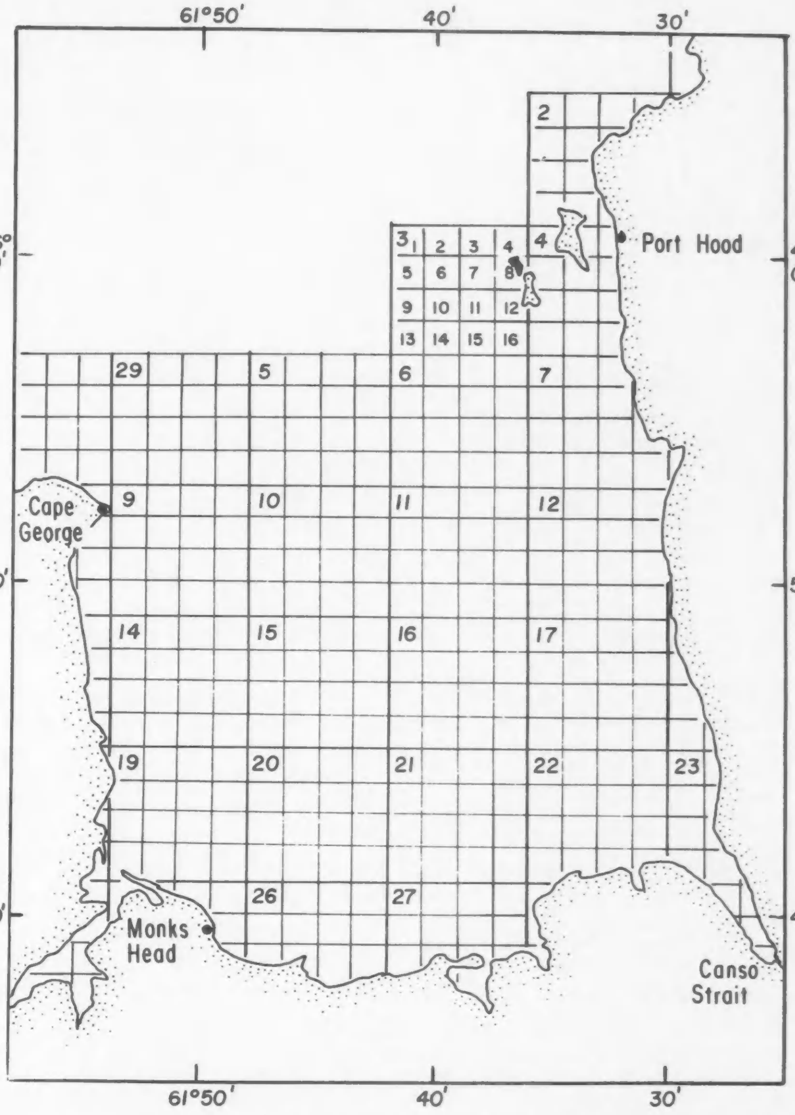

FIG. 1. St. Georges Bay, Nova Scotia, ichthyoplankton sampling grid. Each small square is 1 × 1 nautical mile. Stations were choosen randomly: 1973 (variable number), 1974 (16), 1975 (12), 1976 (9), 1978 (15). See Lambert et al. (1982) for locations. From late May to early September there were 10 sampling periods in 1973, 1974, and 1976, 11 in 1975, and 5 in 1978.

in a clockwise gyre at speeds of 5–10 cm/s. The strength of the currents in the gyre decrease with depth. A numerical model developed by Petrie and Drinkwater (1978) suggests that this feature is driven by an eastward along-shore flow in Northumberland Strait across the mouth of the Bay. Normally about 63% of the water volume is exchanged about once per month during June–September. However, energetic low frequency events, such as storms, are capable of flushing the volume in a few days. Barring such events, passively drifting organisms such as mackerel eggs and early larvae can be expected to maintain themselves within the gyre on a time scale exceeding 30 d (Drinkwater 1978). This is particularly important because the life history stages we were following spanned about 15 d, on average.

Variability

Many of the physical characteristics of St. Georges Bay were remarkably constant during the study (Table 1). For instance, the between-year variability, expressed as the coefficient of variation (CV) for the period when the sea surface temperature exceeds 8°C (which we call the mackerel season), the mean temperature during this period, and the duration of the first growing season vary only 2–8% with respect to the 6-yr mean.

TABLE 1. Selected thermal and mixed layer characteristics of St. Georges Bay, 1973–78.

	Mackerel season[a]			First growing season[b]			Sea surface[c]				Mixed layer[d]		
								Maximum temp.					
Year	Duration (d)	Mean SST (°C)	Degree days	Duration (d)	Mean SST (°C)	Degree days	Rate of warming (°C/d)	°C	Day	Rate of cooling (°C/d)	Rate of increase (m/d)	Mean depth (m)	Mean volume ($\times 10^9$ m^3)
1973	163	14.87	2423	139	15.41	2142	0.22	20.5	219	−0.12	0.04	9.7	9.6
1974	161	14.86	2393	120	15.76	1891	0.14	20.0	229	−0.14	0.23	11.1	10.9
1975	163	15.46	2521	145	16.03	2324	0.31	20.5	205	−0.11	0.24	11.9	11.6
1976	164	15.32	2513	147	15.88	2335	0.13	19.3	237	−0.15	0.15	10.7	10.6
1977[e]	175	14.38	2517	(140)	(15.41)	(2158)	0.20	20.8	221	−0.15	0.14[f]	—	—
1978[g]	168	14.46	2429	133	15.53	2065	0.18	20.6	226	−0.13	0.23	—	—
Mean	166	14.89	2466	137	15.72	2151	0.20	20.3	223	−0.13	0.17	10.9	10.7
S	5	0.44	57	11	0.25	186	0.07	0.55	11	0.02	0.08	0.91	0.83
S/mean	0.03	0.03	0.02	0.08	0.02	0.09	0.35	0.03	0.05	0.15	0.46	0.08	0.08

[a] Period when the sea surface temperature (SST) exceeds 8°C.
[b] Period from peak spawning to autumn migration (SST = 8°C).
[c] June to November inclusive.
[d] June to August inclusive.
[e] Only two stations and only SST.
[f] After Drinkwater and Taylor (1980, p. 4).
[g] Only one station.

TABLE 2. Mackerel spawning cycle characteristics, incubation time, and egg mortality rate, St. Georges Bay, 1973–79.

	First appearance			Appearance of 8°C isotherm		Peak spawning			Spawning cycle				Mean incubation time (D_T, d)	Egg mortality rate (M, d^{-1})[d]
										Julian day				
Year	Julian day	Date[a]	SST (°C)	Day	Date	Day[b]	Date	SST (°C)	Duration (d)	Begin	End	Mean temp.[c]		
1973	157	June 6	8.0	157	June 6	176	June 25	13.1	72	157	229	13.4	5.6	0.564
1974	—	—	—	156	June 5	193	July 12	15.0	67	164	231	14.6	4.8	0.400
1975	—	—	—	162	June 11	175	June 24	12.5	61	163	224	14.4	4.9	0.734
1976	146	May 26	6.5	153	June 1	163	June 11	12.3	70	153	223	13.0	5.9	0.404
1977	149	May 29	7.6	149	May 29	—	—	—	—	—	—	—	—	—
1978	157	June 6	8.0	149	May 29	178	June 27	12.7	71	156	227	13.4	—	—
1979	145	May 25	—	—	—	—	—	—	—	—	—	—	—	—
Mean	151	May 31	7.5	154	June 3	177	June 26	13.1	68	159	227	13.8	5.3	0.526
S	5.8	—	0.7	5.0	—	10.7	—	1.09	4.4	4.7	3.3	0.7	0.53	0.159
S/mean	0.04	—	0.09	0.03	—	0.06	—	0.08	0.07	0.03	0.01	0.05	0.10	0.30

[a] Reported by local trap net fishermen. The nets were set late in 1974 and 1975, so the date of first appearance was not available.
[b] Estimated from production curves for stage I eggs which are roughly 18 h old (see Tables A1–A4).
[c] Mean temperature during spawning cycle weighted by production estimates, and duration of stage I to III eggs (Tables A1–A4).
[d] Estimated by fitting adjusted production of stage I to 3.2 mm (Tables A1–A4) to the equation $Y_i = Y_0 \exp(-Mt)$ where t is the mean age since fertilization and i is the developmental stage.

In fact, 10 of the 13 characteristics listed in Table 1 exhibit a CV <10%.

In contrast, the CV for the heating and cooling of the mixed layer and the rate it increases in depth range from 15 to 46%. It is of interest that St. Georges Bay seems to gain heat at a faster rate (mean = 0.2°/d) than other locations in the southwestern Gulf of St. Lawrence during June to mid-August. By comparison, the long-term mean rate of warming at Entry Island was 0.15°/d (CV = 21%) and 0.12°/d (CV = 21%) at Port Borden, P.E.I., from 1951 to 1973. Drinkwater (1978) noted that year-to-year variations in solar radiation and intensity of mixing are responsible for annual differences in the rate of heating. This turns out to be an important characteristic which we will return to later.

Spawning Migration

It has been known since Goode (1885) that mackerel first appear along the Northwest Atlantic coast when the sea surface temperature reaches 7–8°C in the spring. Sette (1950) observed that the first catches of the season off New England in the late 1920's and early 30's varied as much as 10 d from each other, but only 2 d from the time when the surface temperature had warmed to 7.2°C. He concluded that water temperature has a limiting rather than causal influence on the movements of mackerel, in the sense that they are prevented from entering coastal waters before the surface warms to 7°C, but do not necessarily appear at this temperature.

In the southern Gulf of St. Lawrence, mackerel first appear,

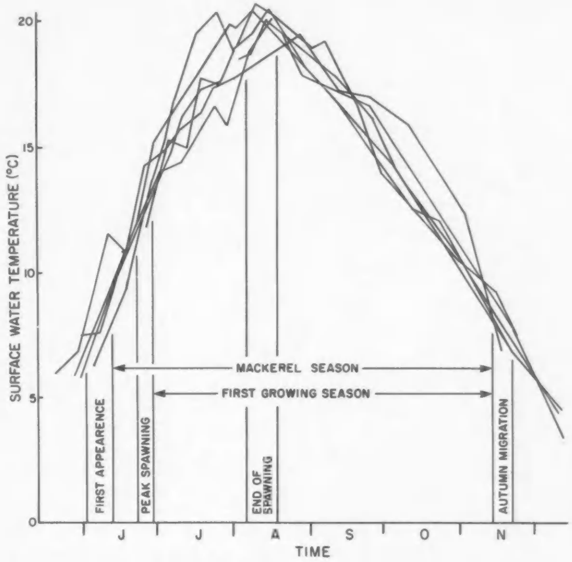

FIG. 2. Timing and duration of major life history events with respect to seasonal trends in water temperature in St. Georges Bay, 1973–78.

on average, when the temperature is 7.5°C (Table 2). Between 1973 and 1979 the time of arrival varied as much as 11 d from each other, but only ±8 d from the appearance of the 8°C isotherm. Though these observations are not as striking as Sette's, they still support his conclusion that the movements of mackerel are closely linked to water temperature.

The timing and duration of various events in the life history of mackerel in relation to the seasonal trend in temperature are illustrated in Fig. 2. Mackerel frequent St. Georges Bay from late May until early November, when the autumn migration appears to be triggered by a falling surface temperature approaching 8°C. Spawning occurs only on the rising phase of the temperature cycle, and normally peaks about 26 d after the date of first appearance (May 31). The first growing season, defined as the period from peak spawning to a surface temperature of 8°C in the autumn, spans about 137 d (Table 1).

The timing of peak spawning and the duration were remarkably similar between years (Table 2). The exception was 1974 when the peak was 16 d later than usual and was centered around a mean temperature of 15°C, instead of 13°C (Fig. 3). This anomaly is difficult to explain: although the rate of heating in June 1974 was below normal, it was the same in June 1976, when peak spawning was earlier than usual. This suggests that the delay in 1974 was caused by some peculiarity in the water masses, and movements of mackerel schools outside, rather than inside, St. Georges Bay.

Early Development

Incubation and Hatching

Lanctot's (1980) observations on incubation times indicate that Atlantic mackerel require temperatures above 7°C for successful development. At 13°C the eggs hatch in about 5.9 d (142 h) compared with 2.9 d (69 h) at 20°C (Appendix A). Over this range in temperature the Q_{10} is about 2.8.

At hatching, Atlantic mackerel average about 3 mm standard length and have a well-defined yolk sac which extends under the head; the eyes are large and unpigmented. At the end of the prolarval stage they are 4 mm in length and have well-formed mouths and fully pigmented eyes. During early development the larvae undergo a major change in body form which probably enhances their success in capturing active prey and in avoiding predators. At birth they have a fineness ratio (standard length/maximum width) around 16. During the prolarval and first-feeding stages growth is directed proportionally more to width, so by the 10-mm stage the fineness ratio has fallen to 6.5. By comparison, a fully grown specimen has a fineness ratio near 4.6. The fact that this species develops a streamlined form so early in life suggests that they are capable of moving at high speeds when the need arises, and has obvious implications concerning net avoidance (see Appendix B).

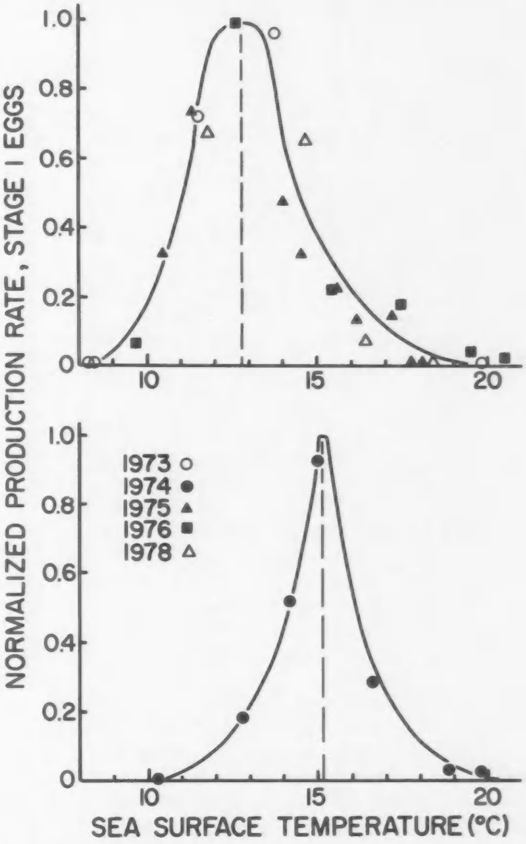

FIG. 3. Production rates of stage I eggs. Peak production normally occurs at 13°C; 1974 was an abnormal year.

Vertical Distribution

Routine sampling during 1974–76 demonstrated that mackerel egg concentrations $N(i, z)$ tended to decline exponentially with depth in the top 5 m (Fig. 4). This relationship can be described by the following equation:

$$N(i, z) = N(i, o) \exp (b(i)Z) \qquad (1)$$

where i is the development stage, Z is the depth (metres), and $b(i)$ and $N(i, o)$ are fitted constants for each stage and sampling

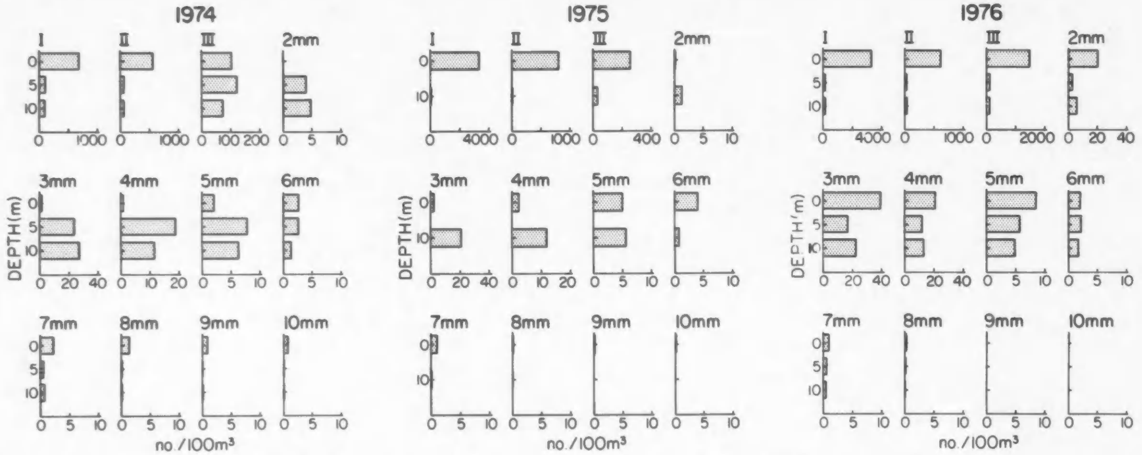

FIG. 4. Seasonally weighted concentrations (no./100 m^3) of stages I to 10 mm at surface and 5 and 10 m. Note: sampling was conducted at night in 1976.

period. Figure 5 shows that the rate constant $b(i)$ in Eq. 1 was a decreasing function of the temperature gradient in the top 5 m.

Further examination of the most extensive data record (1976) revealed that the largest mackerel eggs that appear early in the spawning season were associated with large, negative values of $b(i)$. This observation suggests that large eggs have a lower density than smaller eggs and thus will tend to be more concentrated near the surface, particularly under light winds when vertical mixing is reduced. The measured size of stage I eggs at all depths in 1976 supports this interpretation, since the mean diameter was largest at the surface, whereas at 5 and 10 m the means tended to be smaller and virtually identical in each sampling period:

Mean diameter (mm) stage I eggs

Date	0.1 m	5 m	10 m
June 1	1.323	1.311	1.306
June 7	1.273	1.261	1.279
June 14	1.221	1.208	1.200
June 21	1.205	1.179	1.192
June 28	1.163	1.150	1.141
July 5	1.154	1.132	1.141
July 14	1.116	1.099	1.112
July 19	1.098	1.092	1.094
July 26	1.094	1.092	1.084
August 2	1.097	1.094	1.091

A multiple regression analysis of the seasonal trends in egg size and the temperature gradient in the top 5 m in 1974 and 1976 demonstrated that these factors explain 70% of the variance in $b(i)$, with each factor accounting for 35%:

$$b(i) = 1.55 - 1.60\bar{D} - 0.35\Delta T$$

where $\bar{D}$ = mean diameter (millimetres) stage I eggs and ΔT = temperature gradient (degrees Celsius) between surface and 5 m. Of all possible combinations of the aforementioned variables and interaction terms, this equation gave the best fit.

In contrast, in the 5–10 m layer all egg stages were either evenly distributed or else showed a slight linear decline in concentration with depth. This decline, when it occurred, was also negatively correlated with the temperature gradient. Sette (1943) reported that mackerel eggs have a tendency to sink gradually as development proceeds, so that the late stages are found deeper than the early ones, but not below the thermocline. Accordingly, in estimating the production rates, we assumed that the concentration of all stages decreased linearly with depth below 10 m, reaching zero at the top of the thermocline where the discontinuity in water temperature and density was sharpest.

Median Depth

Our observations of vertical distribution are in broad agreement with Sette's (1943). Figure 6 shows that the seasonal median depth (weighted by the production rate) increased during the incubation period at an average rate of 1.1 (1974), 1.2 (1975), and 0.7 (1976) m/d, which explains why newly hatched larvae were found primarily between 5 and 10 m during daylight (Fig. 4). As the larvae grew, however, they gradually rose toward the surface at an average rate of 0.6 (1974) and 0.8 (1975) m/d so by the 8-mm stage most larvae were found in the top 5 m.

In this context, it is significant that the largest plankton also occur near surface during the day and decrease progressively in size down to 10 m (Lambert et al. 1982). This pattern was less evident during the night sampling in 1976, when the newly hatched larvae and first-feeding stages were dispersed more uniformly in the top 10 m (Fig. 4). A 24-h time series of neuston samples taken in 1977 resolved this anomaly. From day to night, the mean size of zooplankton decreased from 880 to 770 μm, while the mean size of mackerel larvae fell from 6.4 to 4.7 mm. Since the biomass of the larvae and plankton increased during the night, we concluded that smaller organisms move to the surface at night and return to depth during daylight. The day/night size compositions of larvae also suggest a movement of >8 mm larvae away from the surface at night and a return during the day, when mackerel tend to feed (Last 1980).

Feeding Behavior

An examination of the gut contents of 66 larvae caught in July 1973 indicated that the 50% threshold for the onset of feeding was 3.8 mm (Fig. 7), which is remarkably close to the 50% threshold of 3.6 mm reported for Pacific mackerel (*Scomber*

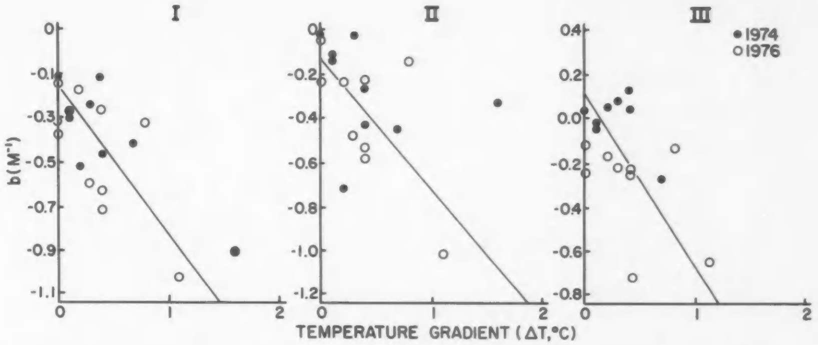

FIG. 5. Dependence of rate constant $b(i)$ describing the exponential decline in the concentration of stage I–III eggs (Eq. 1) on the temperature gradient (maximum–minimum) in the top 5 m. Note that data for only 9 out of 10 sampling periods are plotted in 1974 because only a few mackerel eggs were found in the last period (so it was not included). In addition to this, no stage III eggs were found in the first sampling periods in 1974 and 1976, and no stage II eggs were found in the first sampling period in 1976. This explains the number of data points in each panel.

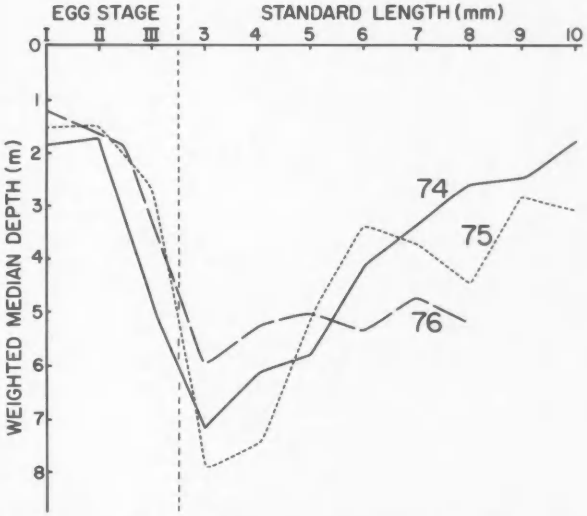

FIG. 6. Seasonally weighted median depth of stages I to 10 mm. Notice tendency for larvae >6 mm to be deeper in the mixed layer at night (1976).

japonicus) (Hunter and Kimbrell 1980). By the 4.5-mm stage all of the St. Georges Bay larvae had been feeding, and their yolk reserves were completely exhausted.

In general, the diet reflected the relative abundance and distribution of available zooplankton in St. Georges Bay (Lambert 1980): copepods predominated and the cladoceran *Evadne* sp., common only in surface waters, was a major food item. By the 8-mm stage, mackerel began to eat other fish larvae including conspecifics: 58% of the mackerel we examined between 8 and 25 mm contained fish larvae, 20% of which were mackerel. The largest cannibal that we found was 15.2 mm, which is interesting, since Hunter and Kimbrell (1980) reported that cannibalism in laboratory-reared *S. japonicus* started at 8 mm and ended at 15 mm, when schooling behavior began. Other identifiable fish remains included white hake (*Urophycis tenuis*) and four-beard rockling (*Enchelyopus cimbrius*), both of which are abundant in the mixed layer in summer.

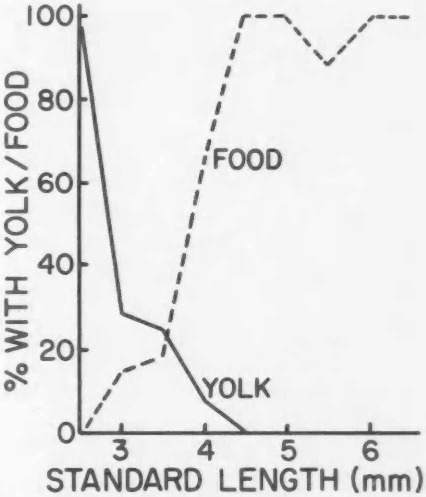

FIG. 7. Duration of yolk sac and first feeding stages, July 1973.

Most prey were smaller than the maximum size mackerel can ingest, as indicated by the occasional large fish larvae in the gut. Figure 8 shows that the mean food width increased steadily at a rate of 42 μm/mm of larval length up to the 10-mm stage; thereafter the rate of increase was much lower (about 13 μm/mm). Since the volume of food ingested followed the same pattern, the observed inflection in food width and volume may indicate the limit to food availability in the mixed layer. The largest copepods in St. Georges Bay have a maximum width of 400–500 μm; if food size is to increase beyond this limit, mackerel must eat fish larvae, which are much rarer than copepods. Thus, our results suggest that during the early larval stages the diet of mackerel reflects the most abundant food species within the available size range, where the maximum is determined by mouth gape. Hunter and Kimbrell (1980) reached a similar conclusion after studying the diet of sea-caught Pacific mackerel. They found that a substantial number of prey eaten were much smaller than the maximum size mackerel larvae are capable of ingesting, and suggested that this may indicate a shortage of large prey in the sea.

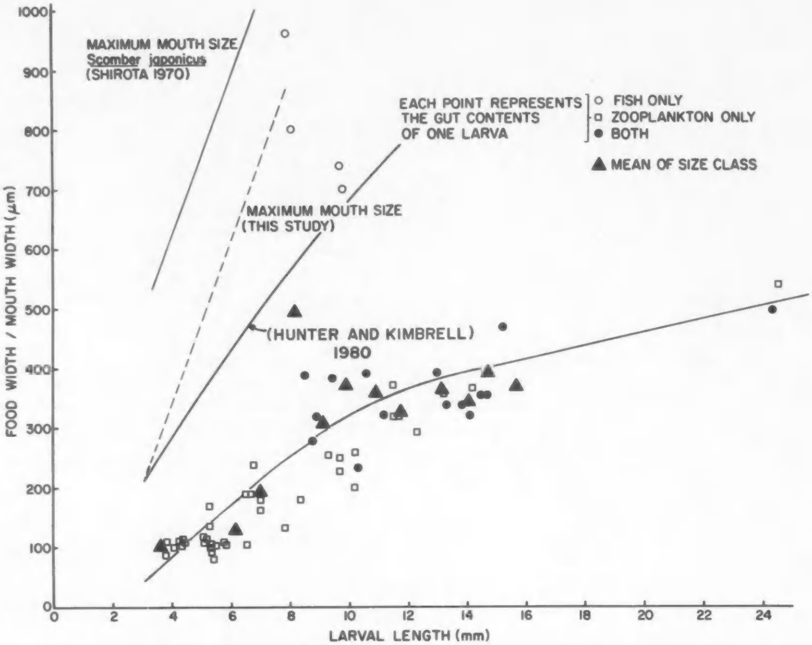

FIG. 8. Relation between mouth width, food width, and mackerel size, July 1973.

In this context, it is worth noting in Fig. 8 that some of the prey consumed by 8- and 9-mm larvae were larger than the mouth widths reported for Pacific mackerel by Hunter and Kimbrell (1980, their fig. 7), but were less than the maximum widths given by Shirota (1970). The largest food sizes we observed suggest that the broken line drawn between these two relationships in Fig. 8 provides an approximate indication of how the maximum, *functional* mouth size increases with body size in *S. scombrus*.

Growth

Larvae

Growth rates during the 3- to 10-mm stages were estimated from the progression in the date of peak abundance of each stage in the samples in 1975 and 1976. The 1974 data were not used because the progression of the modal group was not as clear as it was in the two following years. Standard lengths (millimetres) and weights (milligrams) were fitted to the equations

$$\text{(2a)} \quad W_t = (\alpha bt + W_0^{\,b})^{1/b}$$

and

$$\text{(2b)} \quad L_t = K(\alpha bt + W_0^{\,b})^{1/bd}$$

where t is age (days) since hatching, W_0 is the birth weight (milligrams, wet), α and b are fitted growth parameters (Ware 1975), and $K = (1/C)^{1/d}$, where $W = CL^d$ (see Appendix A). In fitting the data to Eq. 2a and 2b, we first estimated a common value of b for 1975 and 1976 ($b = 0.148$) and then followed standard regression procedures for calculating α in each case.

The water temperature (weighted by the observed duration of each stage) during the progression of the modal group was much warmer in 1975 ($T = 17.4$°C) and the growth rate was higher ($\alpha = 0.414$) than in 1976 when the weighted temperature was 14°C and $\alpha = 0.275$. To obtain an approximate measure of the effect of temperature on the growth rate from birth to 10 mm α was regressed against the weighted temperatures listed above:

$$\text{(3)} \quad \alpha = 0.041\bar{T} - 0.2974.$$

Eq. 3 was then substituted into Eq. 2. In this expanded form, Eq. 2a and 2b can be manipulated algebraically to determine the temperature-dependent duration of each stage, which we require to calculate the larval production rates (see Appendix A).

Although the stage durations obtained by this procedure are only approximate, they are consistent with other findings. For example, one can derive from Eq. 2b and 3 the time newly hatched mackerel larvae require to reach metamorphosis (15 mm) at different temperatures: $t_{15} = 0.87/(0.0061\bar{T} - 0.044)$. Between 16.8 and 22.1°C, Hunter and Kimbrell (1980) found a Q_{10} of 2.2 (note that they inadvertently give a value of 3) for the time *S. japonicus* take to reach metamorphosis. Over the same temperature range the Q_{10} for St. Georges Bay mackerel is 2.3. At an average temperature of 15–17°C, *S. scombrus* grew at a rate of about 0.64–0.81 m/d in St. Georges Bay, which is very similar to the average growth rate from birth to metamorphosis (0.75 mm/d) estimated for the southern component in the middle Atlantic bight (Kendall and Gordon 1981, their fig. 2).

Food Size and Concentration

In addition to temperature, growth in fishes is also regulated by food size and concentration. To evaluate the relative importance of these factors we divided the larvae into two groups: 3–6 mm, which covers the first-feeding stage, and 6–8 mm. Since the abundance of larger particles within the feeding range of each stage should have the strongest influence

TABLE 3. Environmental conditions experienced by first feeding (3–6 mm) and late stage (6–8 mm) larvae. Temperature is based on the observed vertical distribution of larvae and was weighted by the average seasonal duration of each stage (Tables A2–A4). Plankton size and concentration of "optimal" size fraction in each case were weighted by the estimated production rates of each larval group, for each sampling period, over the season. The instantaneous daily mortality rates are also shown.

	3–6 mm larvae					6–8 mm larvae				
Year	Weighted temp. (°C)	Weighted mean plankton size (μm)[a]	Weighted concentration (mg/m^3)[a]	Growth rate (mm/d)	Mortality rate (d^{-1})	Weighted temp. (°C)	Weighted mean plankton size (μm)[b]	Weighted concentration (mg/m^3)[b]	Growth rate (mm/d)	Mortality rate (M, d^{-1})
1974	15.33	254.3	160.4	0.53	0.48	15.47	459.8	229.0	0.63	0.22
1975	16.71	262.6	285.4	0.62	0.60	17.79	470.2	454.5	0.81	0.88
1976	15.42	252.3	142.2	0.53	0.44	15.92	460.5	183.7	0.67	0.66

[a] 80- to 253-μm size fractions only.
[b] 253- to 602-μm size fractions only.

on growth (Hunter and Kimbrell 1980), we defined the "optimal fraction" as the upper half of the feeding range, where the maximum is determined by mouth size (Fig. 8). According to these criteria, the optimal size range for 3- to 6-mm larvae is the 80- to 253-μm fraction of the plankton sampled by the 80-μm net and the 253- to 602-μm fraction for the 6- to 8-mm larvae.

The feeding potential offered by these fractions can be characterized by two statistics: the mean particle size (PS) and the mean concentration $[\bar{P}]$, both weighted by the average production rates of the respective size groups of larvae. These statistics, including the mean temperature ($\bar{T}$) experienced by each size group, and their corresponding growth ($\Delta L/\Delta t$, millimetres per day) and daily mortality rates (M) for 1974–76 are listed in Table 3.

As expected, there was a significant correlation between the growth rate and temperature between 1974 and 1976, in both size groups. There was also a significant positive correlation (r = 0.998) between the food size and food concentration available to the 3- to 6-mm larvae. Although the other possible correlations in Table 3 are not significant, it is interesting to note that the weighted food size and concentration were greater for both size groups in 1975. Hence, the growth rates may have been higher in 1975 not only because of warmer temperatures, but also because there were more large food particles available to mackerel between June and mid-August.

Juvenile Stage

Over the period of study, juvenile mackerel (>15 mm) in their first growing season were captured in St. Georges Bay by various means. The average lengths (±1 SD) of fish from these samples are shown in Fig. 9 and were fitted to a Gompertz equation, using the procedure suggested by Ricker (1979). We choose this equation strictly for its descriptive power, since it provided a remarkably good fit to the observed progression in length. For example, one can calculate from the equation given in Fig. 9 that the average growth rate from birth to metamorphosis is 0.73 mm/d, which compares favourably with the results obtained from Eq. 2b and with Kendall and Gordon's (1981) observations on the southern component.

The strong influence of temperature on juvenile growth is also apparent in Fig. 9, where it can be seen that the maximum growth rate (2.4 mm/d) is very close to the date (August 11) when the mixed layer reaches a maximum temperature (Table 1, column 10). Thereafter the steady diminution in the growth rate can be linked to the cooling of the surface water.

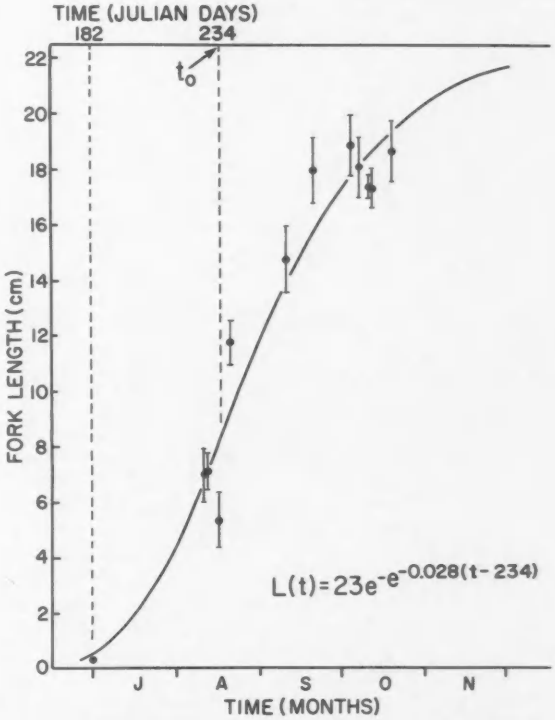

FIG. 9. Mean length (±1 SD) of young of the year mackerel caught by gill nets and by angling in St. Georges Bay. In fitting the gompertz growth equation, we observed that peak spawning is centered around day 177 (June 26) and a mean temperature of 13°C. At this temperature, peak hatching will occur 5–6 d later on day 182 (July 1), which was defined as age zero. The maximum growth rate was in mid-August (day 234). At the end of the first growing season (early November), mackerel average 19–20 cm.

Mortality

In terms of total egg production, the years rank from highest to lowest in the following order: 1973, 1975, 1976, 1974 (Fig. 10; Appendix A). Fifteen days after fertilization the order was 1974, 1976, 1975. To understand the reason for this we must

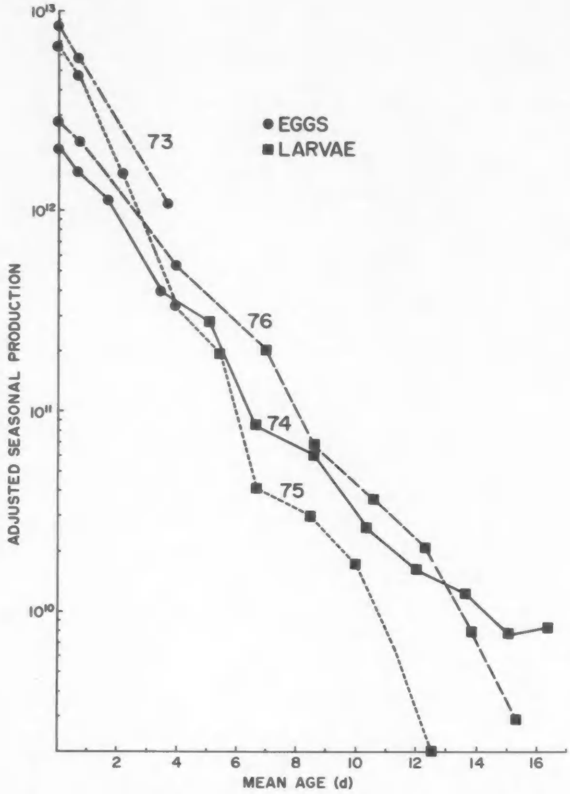

FIG. 10. Survival curves relating total production of stages I to 8 mm to seasonally weighted mean age (see Tables A1–A4).

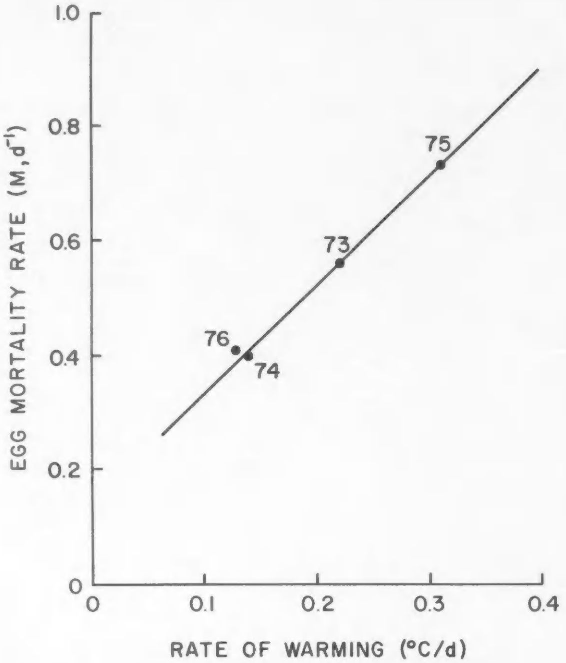

FIG. 11. Correlation between the instantaneous daily mortality rate during incubation and the rate of warming of the mixed layer during the spawning season ($N = 4$, $r = 0.998$, $p < 0.01$).

look more closely at the distribution of the plankton and thermal conditions in St. Georges Bay.

Between 1973 and 1976 the instantaneous egg mortality rate averaged −0.53/d, which represents a decrease in the size of the cohort of about 41%/d. In 1975 the mortality rate was 52%/d, the highest for the 5-yr period (Table 2). Although these rates are high they are not unexpected for a species that spawns pelagic eggs in a water mass with a high temperature. Kendall and Gordon (1981) reanalyzed Settes' data and came up with a comparable daily mortality rate ($M = -0.35$/d) for the southern component of the 1932 year class. Similarly, Ciechomski and Capezzani (1973) reported an average instantaneous mortality rate of −0.6/d at 11–14°C during the period of peak spawning of the Argentinean anchovy (*Engraulis anchiota*).

In relation to the physical variables that were measured, the egg mortality rates were highly correlated with the rate of warming during the spawning season, which was a surprise (Fig. 11; Table 1). Assuming this relationship is not spurious, exactly what it means is unclear: it might reflect a higher incidence of lethal deformities during early development, or more intense predation pressure, due to some structural change in the field of large invertebrates and small fishes that eat pelagic eggs. Unfortunately the effect we are trying to explain is small, since a 10% increase in the rate of warming above the mean corresponds to a 7% increase in the instantaneous mortality rate. The possibility that an increase in the rate of warming somehow enhances the incidence of lethal accidents during the incubation period can be tested experimentally. The possibility that it is due to predation is more likely, but also more difficult to test.

The larval production estimates were adjusted for net avoidance, because the swimming performance of fish larvae increases dramatically with body size and water temperature (Appendix B). In *S. japonicus*, 3- to 5-mm larvae have a burst speed capability of at least 10–15 body lengths (Hunter and Kimbrell 1980). The adjusted production figures (Tables A2–A4) attempt to correct for this effect and, therefore, provide the most reliable mortality estimates.

The mean larval mortality rates (obtained for each year class by pooling the rates listed in column 10 in Tables A2–A4) are not significantly different from the mean egg mortality rates within each year class. In other words, the mortality rate from fertilization to the 8-mm stage was more or less constant. During the period of study the average M ranged from −0.38/d (1974) to −0.69/d (1975). For various reasons,[2] we feel that the 1974 production estimates are the most accurate. On the other hand, because of limitations in the sampling procedure it is possible that the 1975 production estimates are a bit low and, hence, the mean mortality rate is a little higher than it should be. By comparison, we note that Kendall and Gordons' (1981) mortality estimate is only a very rough approximation because of their uncertainty about the growth rate of the 1932 year class. Nevertheless, their estimate ($M = -0.35$/d) and ours are of the same order.

Returning to the problem posed at the beginning of this section, the explanation for the observed variation in survival is complex. In 1975 spawning began at normal temperatures, yet there was a high mortality during the egg stage which we can link to an abnormally high rate of heating of the mixed layer. Larval survival in 1975 was also poor despite the fact that feeding conditions appeared better than in both 1974 and 1976 (Table 3).

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[2] Best coverage (16 stations), extensive number of sampling periods (10), sampled at three depths (0, 5, and 10 m).

An examination of the spatial distributions of the larvae and zooplankton provides a possible explanation for this paradox. In 1974 (good survival) during the period of peak larval production, strong correlations between mean length of larvae and mean size of zooplankton taken in horizontal net tows were found between sampling stations where mackerel were present.[3] However, this was not the case in 1975:

Year	Water layer	r	n	p
1974	Surface	0.49	9	0.10
	5 m	0.61	10	0.05
	10 m	0.76	10	0.01
1975	Surface	−0.03	11	NS
	10 m	0.03	11	NS

The 1976 data cannot be used in this comparison, because samples were taken at night when larvae do not feed and the nocturnal migration complicates matters. Nevertheless at 10 m where the smallest larvae (which move very little) occur there was a good correlation between their size and that of the zooplankton. Thus in 1975 it is possible that isolated clusters of larvae may have experienced good growth and survival; however, *most* size groups may have fared badly on both counts because of the poor match in their spatial distribution relative to the zooplankton.

To sum up, it is impossible to say whether the unseasonally high temperatures and rate of warming in 1975 changed the zooplankton field, and possibly the distribution of predators, or whether it had a more direct effect on larval mortality. Statistically, we found that the larval mortality rate increased with temperature during the period of study (Table 3, $N = 6$, $0.01 < p < 0.05$). Whatever was responsible for the poor survival in 1975, it clearly offset any advantage that normally might have accrued from the high growth rate of the survivors.

Concluding Remarks

The close link between major life history events and temperature implies that mackerel have a keen sense of temperature discrimination which they use to guide their annual migration and spawning activity. Physiologists have demonstrated that teleosts are capable of discriminating a temperature threshold of ±0.05° (Brett 1970). Brett (1970) cautioned, however, that whereas temperature may set narrow limits for spawning there is a complex interaction between temperature and daylength. Notwithstanding this, our results (e.g. Fig. 3) suggest that mackerel use their ability to accurately discriminate temperature, to regulate their spawning activity and oogenesis, so peak spawning occurs at 13°C, and so the size of the first-feeding larvae matches the size composition of the plankton. Mackerel are serial spawners, which mature and release successive batches of eggs during the reproductive period (Morse 1980). In St. Georges Bay both mackerel egg size and plankton size decrease over time and in relation to the ambient temperature (Ware 1977). One of us has argued elsewhere that this decline in egg size is adaptive, since it ensures that the first-feeding stages are an appropriate size, on average, to forage on the dominant sized plankton (Ware 1977). Plankton size and egg size decline at the same rate, thus satisfying the condition that these characteristics change in phase. Instead of being a decisive factor, however, we see this phenomenon as a coarse tuning mechanism which tends to get the first feeding stages off to a good start. To understanding how successful they have been in any given year we must look more closely at the distribution of the plankton in relation to the feeding range of different sizes of larvae. In this context, the increase in median depth during incubation enhances, in the vertical dimension, the match between the size distributions of the first feeding stages and the plankton. We have also shown that this coupling between the sizes of the larvae and the plankton is maintained by the progressive movement of larger mackerel toward the surface (Fig. 6).

It now appears relevant to ask how important are these remarkable adaptations in determining recruitment? In this respect our results are in broad agreement with Sette's (1943; and Kendall and Gordon's reanalysis). Both studies indicate

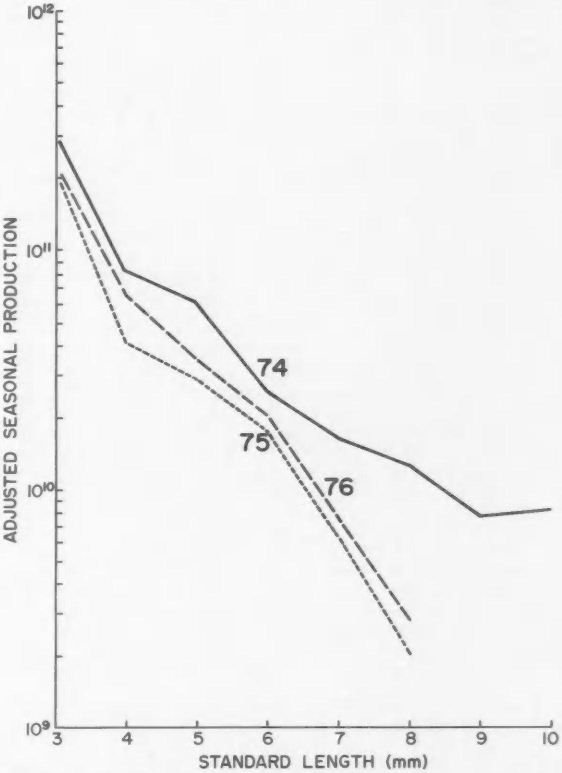

FIG. 12. Size-specific survival curves for 3- to 8-mm stage. Notice that the mortality rate was slightly higher among first feeding larvae (3–4 mm). See text and Tables A2–A4.

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[3] Mean size of zooplankton ($\overline{PS}$) in the horizontal tows was estimated from

$$\overline{PS} = \Sigma\,(W_iS_i)/\Sigma\,W_i$$

where W_i = wet weight of zooplankton on ith screen and S_i = nominal particle width on ith screen. In this case, data for only the 405-, 602-, 860-, and 1050-μm screens were used to calculate $\overline{PS}$ at each depth and station (see Lambert et al. 1982).

that the mortality rate from hatching to the 8-mm stage is roughly constant. It is of interest, however, that mortality during the first feeding stage (3.2–4 mm) was slightly higher in St. Georges Bay in every year class (Fig. 12), suggesting that some larvae have difficulty making the transition to exogenous feeding. On the other hand — and this is the important point — there is absolutely no evidence in our study, nor in Sette's, that mortality during the first feeding stage is a catastrophic event, establishing the general course of recruitment. Instead, the data indicate that survival during the first growing season is determined by a host of factors, which include the temperature, and the distribution, and size composition of mackerel larvae in relation to their food supply (and their predators). Though many questions remain unanswered perhaps we understand a little more clearly, now, how this intricate process operates and how its effects accumulate in the first summer to help establish year class strength.

Acknowledgments

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Appendix A: Production Estimates

Stage Duration

Here we outline the procedure for estimating the annual production of each developmental stage. All larvae were measured to the nearest 0.1 mm in the laboratory and were arrayed into size classes so the midpoint was an integer (e.g. for the 4-mm class the upper and lower limits were 4.5 and 3.6 mm, respectively). The only exception was the prolarval stage: in this case, since the average length at hatching is 3 mm, if the upper class limit is set at 3.5 mm, the resulting midpoint is 3.2 mm.

The duration of the egg and prolarval stages were estimated from Lanctot's (1980) study. Our stage I eggs include her stages 1–5 and spans the period from fertilization to one-half epiboly, where the blastoderm extends halfway around the yolk. Our stage II corresponds to Lanctot's stages 6–8 inclusive and represents the period from one-half epiboly to the point where the length of the embryo covers one-half the circumference of the yolk. Stage III covers the remaining devlopmental events up to and including hatching.

TABLE A1. Mackerel egg production estimates, St. Georges Bay, 1973. All stage durations are temperature dependent.

Stage (i)	Duration (d)	Mean age (d)	Δt (d)	Unadjusted production (P_i)	Weighted mean temp. ($\bar{T}$, °C)	Mortality rate (M, d^{-1})
0	0	0		8.97×10^{12}	—	
			0.78			0.563
I	1.55	0.78		5.78×10^{12}	13.21	
			2.96			0.564
II, III	4.03	3.74		1.09×10^{12}	13.47	
			2.01			
3.2	Hatching	5.92		—		

NOTE: Δt for stage $i = \left(\frac{\text{Duration }(i)}{2} + \frac{\text{Duration }(i+1)}{2}\right)$.

TABLE A2. Mackerel egg and larval production, St. George Bay, 1974. All stage durations are temperature dependent. Adjusted larval production estimates have been corrected for avoidance, where p = probability of capture (Appendix B).

Stage (i)	Weight (mg, wet)	Duration (d)	Mean age (d)	Δt_i (d)	Unadjusted production (P_i)	Weighted mean temp. ($\bar{T}$, °C)	p	Adjusted production (Y_i)	Mortality rate (M, d^{-1})
0	0.823	0	0		2.09×10^{12}	—	1.0	2.09×10^{12}	
				0.64					0.457
I	—	1.28	0.64		1.56×10^{12}	14.6	1.0	1.56×10^{12}	
				1.19					0.235
II	—	1.10	1.83		1.18×10^{12}	14.5	1.0	1.18×10^{12}	
				1.77					0.614
III	—	2.43	3.60		3.98×10^{11}	14.6	1.0	3.98×10^{11}	
				1.65					0.205
3.2 mm	0.140	0.86	5.25		2.73×10^{11}	15.0	0.96	2.84×10^{11}	
				1.50					0.807
4	0.296	2.13	6.75		7.96×10^{10}	15.3	0.94	8.47×10^{10}	
				2.01					0.162
5	0.628	1.88	8.76		5.45×10^{10}	15.4	0.89	6.12×10^{10}	
				1.79					0.485
6	1.159	1.70	10.55		2.13×10^{10}	15.5	0.83	2.57×10^{10}	
				1.62					0.289
7	1.946	1.54	12.17		1.21×10^{10}	15.7	0.75	1.61×10^{10}	
				1.55					0.143
8	3.050	1.55	13.72		8.74×10^{9}	15.0	0.68	1.29×10^{10}	
				1.49					—
9	4.532	1.43	15.21		5.42×10^{9}	15.2	0.70	7.74×10^{9}	
				1.42					—
10	6.459	1.40	16.63		3.74×10^{9}	15.0	0.46	8.13×10^{9}	
									Mean = 0.377

NOTE: $M_i = \log_e (Y_i/Y_{i+1})/\Delta t_i$.

According to Lanctot (her Eq. 6), the duration of each stage in days is

(4a) $D_{\mathrm{I}} = 0.0156/X$

(4b) $D_{\mathrm{II}} = 0.0133/X$

(4c) $D_{\mathrm{III}} = 0.0289/X$

where X is a temperature-dependent coefficient: $X = 0.00149T_M - 0.0096$ (Lanctot 1980, her Eq. 15). When extrapolating to the field, we define T_M as the water temperature at the median depth of each developmental stage during the sampling period. The incubation time is therefore equal to the sum of the three stage durations:

(5) $D_T = 0.058/X$.

Similarly, the duration of the prolarval stage was estimated from Lanctot's equation:

$$L(t) = 5.0 - 2.79 \exp(-Ct)$$

where $L(t)$ = standard length (millimetres) at time t (hours after fertilization) and $C = 0.0024T_M - 0.0203$ (Lanctot's Eq. 19). Hence, the duration of the 3.2-mm stage (in days) is

$$D_{3.2} = \left(\ln \frac{2.79}{5.0-3.5} - \ln \frac{2.79}{5.0-3.0}\right) \Big/ 24C$$

which simplifies to

$$D_{3.2} = 0.012/C.$$

For the postlarval stages, standard lengths were converted to wet weight (milligrams) using the empirical regression

$$W = 0.0028L^{3.363}.$$

There were no significant differences in the length–weight parameters between years, so the data were pooled to obtain the average values shown above. The duration of each millimetre stage i (from 4 to 8 mm) in each sampling period k was then calculated from the equation

$$D_{i,k} = (U_i^b - L_i^b)/\alpha b$$

where U_i and L_i represent the upper and lower class interval weights, $b = 0.148$, and α is defined above by Eq. 2 and 3 — in this case, $\bar{T}$ represents the observed value of T_M, which is the temperature at the median depth of stage i in period k.

Abundance Estimates

The stage abundance during each sampling period was calculated from the observed concentration (number per cubic metre) in three layers: $J(1)$ = 0–5 m, $j(2)$ = 5–10 m, and $j(3)$ = 10 m – thermocline. The mean concentration in each layer, at each station (m), in each sampling period, was multiplied by the volume of the layer in St. Georges Bay to obtain a raised abundance estimate. This procedure produces m independent estimates of the layer totals and the following mean estimate:

$$A_{i,j,k} = \left(\sum_{m=1}^{y} A_{i,j,k,m}\right) \Big/ y$$

where y = number of stations sampled during period k. Next, the total abundance of each stage in St. Georges Bay at time k was obtained by summing the respective layer totals:

$$A_{i,k} = \sum_{j=1}^{3} A_{i,j,k}.$$

In the final step, the daily production rates $P_{i,k}$ were estimated

TABLE A3. Mackerel egg and larval production, St. George Bay, 1975. All stage durations are temperature dependent. Adjusted larval production estimates have been corrected for avoidance, where p = probability of capture (Appendix B).

Stage (i)	Weight (mg, wet)	Duration (d)	Mean age (d)	Δt_i (d)	Unadjusted production (P_i)	Weighted mean temp. ($\bar{T}$, °C)	p	Adjusted production (Y_i)	Mortality rate (M, d^{-1})
0	0.823	0	0		7.35×10^{12}	—	1.0	7.35×10^{12}	
				0.74					0.573
I	—	1.48	0.74		4.81×10^{12}	13.5	1.0	4.81×10^{12}	
				1.36					0.823
II	—	1.23	2.10		1.52×10^{12}	13.7	1.0	1.52×10^{12}	
				1.71					0.886
III	—	2.19	3.81		3.34×10^{11}	15.3	1.0	3.34×10^{11}	
				1.42					0.375
3.2 mm	0.140	0.64	5.23		1.88×10^{11}	17.2	0.96	1.96×10^{11}	
				1.26					1.257
4	0.296	1.87	6.49		3.74×10^{10}	16.4	0.93	4.02×10^{10}	
				1.75					0.169
5	0.628	1.62	8.24		2.63×10^{10}	16.7	0.88	2.99×10^{10}	
				1.52					0.364
6	1.159	1.42	9.76		1.39×10^{10}	17.1	0.81	1.72×10^{10}	
				1.33					0.748
7	1.946	1.23	11.09		4.58×10^{9}	17.8	0.72	6.36×10^{9}	
				1.14					1.015
8	3.050	1.05	12.23		1.18×10^{9}	18.7	0.59	2.00×10^{9}	
									Mean = 0.690

TABLE A4. Mackerel egg and larval production, St. George Bay, 1976. All stage durations are temperature dependent. Adjusted larval production estimates have been corrected for avoidance, where p = probability of capture (Appendix B).

Stage (i)	Weight (mg, wet)	Duration (d)	Mean age (d)	Δt_i (d)	Unadjusted production (P_i)	Weighted mean temp. ($\bar{T}$, °C)	p	Adjusted production (Y_i)	Mortality rate (M, d^{-1})
0	0.823	0	0		2.97×10^{12}	—	1.0	2.97×10^{12}	
				0.78					0.350
I	—	1.55	0.78		2.26×10^{12}	13.2	1.0	2.26×10^{12}	
				3.26					0.445
II, III	—	4.32	4.04		5.30×10^{11}	13.0	1.0	5.30×10^{11}	
				2.72					0.377
3.2 mm	0.140	1.12	6.76		1.90×10^{11}	14.5	0.93	2.04×10^{11}	
				1.61					0.711
4	0.296	2.10	8.37		5.65×10^{10}	15.4	0.87	6.49×10^{10}	
				1.97					0.306
5	0.628	1.84	10.34		2.73×10^{10}	15.6	0.77	3.55×10^{10}	
				1.72					0.316
6	1.159	1.60	12.06		1.32×10^{10}	16.0	0.64	2.06×10^{10}	
				1.56					0.616
7	1.946	1.52	13.62		3.86×10^{9}	15.8	0.49	7.88×10^{9}	
				1.44					0.697
8	3.050	1.36	15.06		8.66×10^{8}	16.1	0.30	2.89×10^{9}	
									Mean = 0.477

by dividing the total abundance $A_{i,k}$ by the corresponding stage duration $D_{i,k}$.

The resulting production rates were then plotted for each period; adjacent points were joined by a straight line and the peak abundance was estimated by extrapolation. The seasonal production P_i, summarized in Tables A1–A4, was obtained by calculating the area under each curve. Notice that the stage durations and ages represent annual means, weighted by the corresponding production rates in each period. The adjusted production figures were corrected for avoidance (Appendix B) and are believed to be the most reliable estimates.

Variance

The variance of the total abundance of stage i in period k, $V_{i,k}$, can be obtained by calculating the variance of the station estimates for each layer ($A_{i,j,k,m}$). Variances are additive so the variance of the estimate $A_{i,k}$ is

$$V_{i,k} = \sum_{j=1}^{3} V_{i,j,k}.$$

The following table summarizes the sampling variance, expressed as the coefficient of variation (percent), for each stage during the period of peak abundance:

Stage	1974	1975	1976
I	33	25	19
II	54	23	22
III	23	34	23
3.2	15	24	31
4	15	20	20
5	22	29	20
6	35	32	15
7	39	32	22
8	69	57	38
9	65	64	50

Three points are evident: (1) the within-year pattern indicates that all stages are contagiously distributed (variance > mean); however, (2) presumably as a result of diffusion and other dispersive forces operating during the incubation period the first feeding stages tend to be more evenly distributed (lowest CV); (3) the variance was highest for the largest larvae. Since the probability of avoidance also increases with size, the production estimates for larvae >8 mm are probably not very accurate.

Appendix B: Correction for Avoidance

Here we extend the argument proposed by Clutter and Anraku (1968) to estimate how the probability of capture varies with larval size and temperature. Clutter and Anraku determined that the probability of capture (p) can be approximated by:

$$(6)\qquad p = 1 - \frac{1}{\Pi R^2}\left(a(R^2 - a^2/4)^{1/2} + 2R^2 \sin^{-1}(a/2R)\right)$$

where a = distance (centimetres) the larvae move between the time they react to the net and the time it reaches their plane and R = radius of the net (centimetres).

The burst speeds of fish $U_{\max}$ (centimetres per second) depend on body length (L, centimetres) and temperature; hence, the distance (a) in the capture equation is a size- and temperature-dependent variable. Experiments reported by Blaxter (1969) on herring larvae indicate that

$$(7)\qquad U_{\max} = fL^{\beta}$$

where $\beta = 2.42$ and f is a temperature-dependent coefficient.

Fish larvae probably react to pressure waves (i.e. low frequency vibrations and sound waves) and acceleration fronts extending up to 1.5 m in front of a towed net (Clutter and Anraku 1968). The time (T_r) they have to avoid the gear therefore should be independent of their size. Accordingly, the distance moved in time T_r is

$$(8)\qquad a = QL^{\beta}$$

where $Q = T_r \cdot f$.

Equation 6 states that the probability of capture approaches zero as a approaches the net diameter ($2R$). Assuming the length exponent in Eq. 8 is about 2.42 for mackerel, the largest larvae that can be captured ($L_{\max}$) was estimated by substituting $2R$ for a in Eq. 8 and rearranging it to obtain

$$(9)\qquad L_{\max} = (2R/Q)^{0.41}.$$

Fortunately for any specified net and towing speed the coefficient Q can be estimated from the catch data. As a case in point the size frequency distribution of mackerel larvae captured during 1974 is shown in Fig. B1.

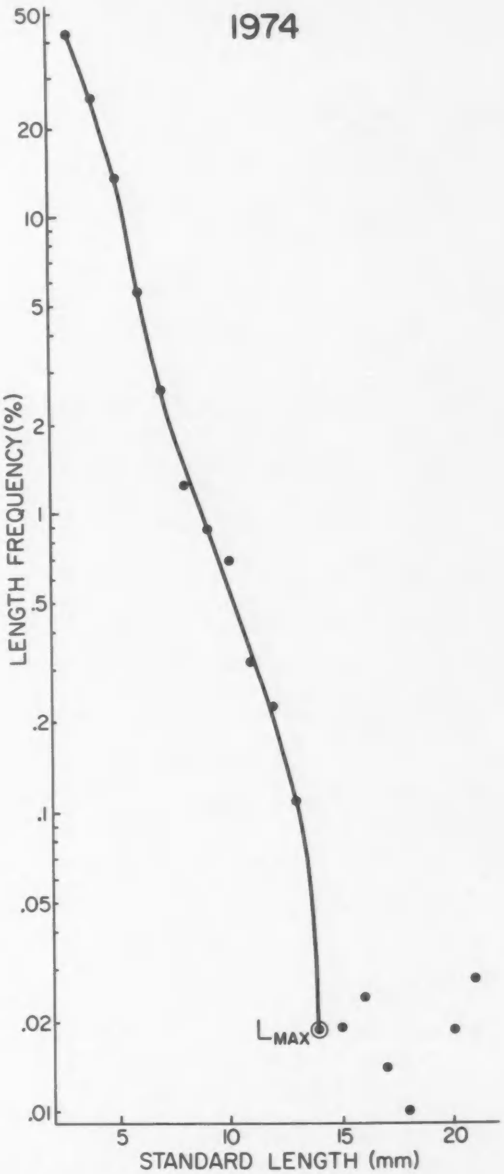

FIG. B1. Normalized catch curve for 1974, combining all samples.

Notice that the relative abundance of the different size classes in the catch declines fairly smoothly until the 13-mm stage. The frequency of larger larvae is demonstrably low and erratic, and presumably represents incidental by-catch. Hence, $L_{\max} \sim 1.4$ cm, which means that $Q \sim 22$. Analysis of the 1975 and 1976 catch data yields similar values.

To account for the effect of water temperature we assumed a Q_{10} of 2. Since $Q = 22$ when the water temperature was 15°C, at 25°C $Q = 44$. Using a two-point regression we obtain

$$(10)\qquad Q = 7.8 \exp(0.069T)$$

where T is the ambient temperature.

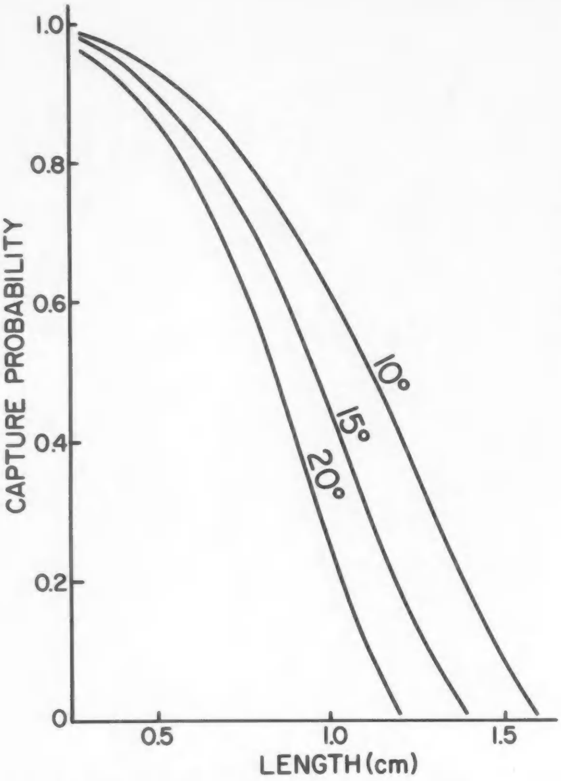

FIG. B2. Estimated change in probability of capture with water temperature and mackerel size.

The probability of capture can now be estimated by combining Eq. 10 and 8 and substituting the result into Eq. 6 for (a).

The corresponding capture curves for 0.3- to 1.6-cm larvae at three temperatures are illustrated in Fig. B2.

Although the Clutter–Anraku equation is acceptable for our purposes, it oversimplifies the escapement process by assuming that all larvae are either left- or right-handed. This constraint demands a high burst speed to explain the observed value of $L_{\max}$. However, if fish larvae detect directional cues and take the shortest route to avoid a net, then the probability of capture will approach zero as a approaches the net radius, and the critical burst speed $U_{\max}$ will be reduced by a factor of 2. In reality the truth undoubtedly lies somewhere between these two extremes, i.e. $p \rightarrow 0$ when

$$R/T_r < U_{\max} < 2R/T_r.$$

Though this method for correcting for avoidance is undeniably primitive, it may be more realistic than adjustments based on day/night catch ratios, and is certainly better than pretending that net avoidance is not a problem.

Water Temperature as the Primary Influence on Timing of Seaward Migrations of Atlantic Salmon (*Salmo salar*) Smolts

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Using multiple regression models we tested if water temperature, water flow, cloudiness, and lunar cycle were significantly correlated with the timing of the yearly descent of Atlantic salmon (*Salmo salar*) smolts in the Norwegian Imsa River, 1976–83. Water temperature between 9 April and 16 May explained 91, 95, and 89% of the yearly variation in date of 25, 50, and 75% cumulative smolt descent, respectively. The regression models were not very sensitive to variations of which date we started and stopped recording the temperature. The start of the yearly smolt run was not triggered by a specific water temperature or a specific number of degree-days, but was controlled by a combination of temperature increase and temperature level in the river during spring. There was no significant correlation between smolt descent and any of the other environmental variables tested.

À l'aide de modèles de régression multiple, les auteurs ont tentéd'établir si la température de l'eau, le débit, la nébulosité et le cycle lunaire étaient en corrélation significative avec le moment de la dévalaison annuelle des saumoneaux de saumon atlantique (*Salmo salar*) dans la rivière Imsa (Norvège) de 1976 à 1983. Entre le 9 avril et le 16 mai, la température de l'eau expliquait respectivement 91, 95 et 89 % de la variation annuelle de la date de 25, de 50 et de 75 % de la dévalaison cumulative. Les modèles de régression n'étaient pas très sensibles aux variations des dates du début et de la fin de l'enregistrement de la température. La descente annuelle des saumoneaux n'était pas provoquée par une température de l'eau ou un nombre de degrés-jours précis, mais elle était régie par une combinaison d'une augmentation de la température et d'un bilan calorimétrique du milieu fluvial au printemps. Il n'y avait aucune corrélation significative entre la dévalaison des saumoneaux et les autres variables environnementales évaluées.

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Each spring, smolts of Atlantic salmon (*Salmo salar*) migrate downstream from nursery areas in freshwater to feeding areas in the sea. Photoperiod during spring has been identified as the major environmental variable controlling the transformation from stream-dwelling parr to seaward-migrating smolts (Wedemeyer et al. 1980), although temperature also affects the timing of the smoltification (Clarke et al. 1981). Water temperature, water flow, cloudiness, and lunar cycle are independent environmental variables that have been suggested to regulate the timing of the seaward migration of smolts (Foerster 1937; White 1939; Österdahl 1969; Baglinière 1976; Solomon 1978; Grau 1982). In Atlantic salmon there have been no published quantitative estimates showing how these variables influence the timing of the smolt run (Solomon 1982). We therefore tested if subsets of these predictor variables could explain yearly variations in timing of the seaward migration of Atlantic salmon smolts during 8 yr in a Norwegian river.

Methods

The study was carried out in the Imsa River near Stavanger, southwestern Norway, 1976–83. Atlantic salmon inhabit the lower 1 km of the river, but not the lakes farther upstream. There is no regular spring spate in the river: the water discharge varies usually between 2.5 and 4.0 $m^3 \cdot s^{-1}$ during April and May. Freshets in water discharge occurred 17–25 April 1976 (maximum discharge: 7.7 $m^3 \cdot s^{-1}$) and 3–20 May 1982 (8.3 $m^3 \cdot s^{-1}$) due to periods of heavy rain fall. The habitat and fish community are further described by Hansen et al. (1984). A Wolf fish-trap

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TABLE 1. Regression of the natural logarithm of temperature ($\log_e t$) on days after 9 April (X_d), correlation coefficient (r), yearly number of descending smolts in the fish-trap, and observed and predicted date in May of 50% descent of Atlantic salmon smolts in the Imsa River.

Year	Temperature equation	r	Number of smolts	Observed date	Predicted date
1976	$\log_e t_{76} = 0.0247X_d + 1.427$	0.96	3144	17	17
1977	$\log_e t_{77} = 0.0255X_d + 1.314$	0.97	2003	21	21
1978	$\log_e t_{78} = 0.0269X_d + 1.380$	0.95	1517	17	18
1979	$\log_e t_{79} = 0.0166X_d + 1.386$	0.92	1428	25	25
1980	$\log_e t_{80} = 0.0368X_d + 1.331$	0.96	1250	13	12
1981	$\log_e t_{81} = 0.0200X_d + 1.535$	0.95	2751	15	17
1982	$\log_e t_{82} = 0.0152X_d + 1.595$	0.80	675	19	18
1983	$\log_e t_{83} = 0.0236X_d + 1.488$	0.98	1482	16	16

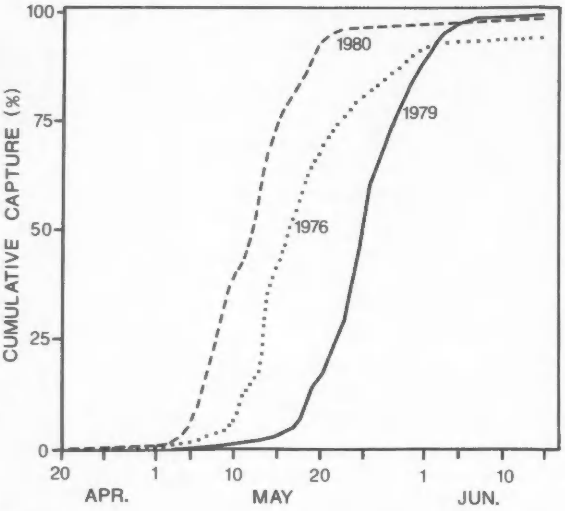

FIG. 1. Cumulative capture of descending Atlantic salmon smolts in the fish-trap in the Imsa River in a year with early, medium, and late smolt descent.

(inclination 1:10, apertures 10 mm) 100 m above the estuary catches all descending smolts larger than approximately 10 cm. The number of descending smolts was registered every day during 8 yr together with water temperature and water flow at 08:00 in the morning, and cloudiness and moon phase during the night. We tested possible multiple regression models between the studied environmental variables during spring and the date of 25, 50, and 75% yearly cumulative smolt descent, using statistical computer programs from SAS (Ray 1982).

Results

More than 90% of the smolts each year descended the river during 1 mo in spring (Fig. 1), although downstream-migrating juvenile salmon were registered in the fish-trap all months of the year. During 1976–83, the date of 50% yearly cumulative smolt descent varied between 13 and 25 May. We found no significant correlations between smolt descent and water flow, cloudiness, and lunar cycle during spring. But water temperature and smolt descent were highly correlated. Using the date in May of 50% cumulative smolt descent ($Y_{50\%}$) as the dependent variable, the variations in downward migration could best be explained by variations in water temperature between 9 April and 16 May (eq. 1), expressed by the regression coefficient (X_r) and the intercept (X_i) in the log-transformed temperature equations (Table 1):

$$(1) \quad Y_{50\%} = 89.6 - 38.2X_i - 718X_r$$

$$R^2 = 0.95,\ P_i = 0.0006,\ P_{X_i} = 0.0015,\ P_{X_r} = 0.0001.$$

Equation 1 explains 95% of the total variation in $Y_{50\%}$. Parallel models based on daily water temperatures between 9 April and 16 May were fitted for 25% ($R^2 = 0.91$) and 75% ($R^2 = 0.89$) cumulative smolt descent. The regression models were not very sensitive to which date we started and stopped recording water temperature. Models estimating $Y_{50\%}$ with high precision ($R^2 > 0.89$) could be fitted using data on daily water temperatures from any date between 15 March and 15 April to any date between 10 May and 1 June.

Discussion

In sockeye salmon (*Oncorhynchus nerka*), Foerster (1937) found significant correlations between mean temperatures for the months January, February, and March and the time of the year when 20% of the seaward migration of the smolts occurred. In Atlantic salmon, several authors have considered water temperature to be important for the start of the seaward migration of smolts (e.g. White 1939; Österdahl 1969; Baglinière 1976; Solomon 1978), but in most earlier studies, the water temperature has not been fully recorded (Solomon 1982), or the authors have looked for temperature thresholds starting the run. In the Imsa River the smolt run started (defined as the day when 5% of the yearly smolt descent were caught in the fish-trap) at temperatures between 5.8 and 11.2°C, 1976–83. Our results indicate that the timing of the smolt descent was not triggered by a specific water temperature or a specific number of degree-days, but was controlled by a combination of actual temperature and temperature increases in the water during spring.

In some rivers, the seaward smolt migrations coincide with increases in water discharge (White and Huntsman 1938; Allen 1944; Österdahl 1969; Baglinière 1976; Raymond 1979; review in Northcote 1984). This might be because water temperature and discharge increase concurrently. Strong spates in water discharge might also flush smolts downstream (Northcote 1984). Furthermore, smolts passing through lakes may have difficulties with finding the outlet if the current velocity is very low (Thorpe et al. 1981; Hansen et al. 1984). If so, freshets or spates in river discharge might influence the timing of the smolt descent. Thus, in some systems smolt descent and water discharge may be correlated, even though no such correlation was demonstrated in the Imsa River.

The present study indicates that cloudiness and lunar cycle are not influential on the timing of the smolt run. Although hypothesized in the literature (Österdahl 1969; Grau 1982), we have not found data from any other river demonstrating significant effects of these environmental variables on timing of the smolt descent.

Our results indicate that naturally or artificially charged temperature regimes of rivers can change the timing of smolt runs, with severe effects on salmon stocks. The reason for this is that survival of salmon in the sea depends partly on the time when the smolts enter the sea. Delayed downstream migration of smolts in the Imsa River resulted in decreased survival to adults (Hansen 1985). Irish data also support that delayed smolt migration can reduce survival of the salmon in the sea (Cross and Piggins 1982). Successive smolt plantings in Sweden showed that a short period during spring was the optimal time for smolts to leave freshwater (Larsson 1977). Dams and impoundments that change the temperature conditions during spring can therefore indirectly affect the survival of salmon. Thus, the smolt run timing–temperature relationship demonstrated in the present paper has implications both for fisheries science and management.

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A Method for Measuring Horizontal Transport of Organic Carbon Over Sediments

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Prewashed, precombusted sand from a sheltered beach in Nova Scotia was returned to the beach at low tide in metal pans. Hourly sampling of pans during high tide was used to assess gross deposition of organic carbon to the bed, with sampling at successive low tides to derive net deposition rate. Resuspension was considered to be the difference between gross and net deposition. Short-term burial of carbon was measured by vertically sectioning pan samples. The results indicate that due to resuspension, the rate of net deposition over 2d (11 $gC \cdot m^{-2} \cdot h^{-1}$) was only 42% of the rate of gross deposition that occurred during a single high tide. The method is useful because it can resolve the short-term particle fluxes that may be trophically important to benthic communities.

Du sable brûlé et prélavé recueilli sur une plage abritée de la Nouvelle-Écosse y a été déposé à nouveau dans des plats métalliques, à marée basse. Un échantillonnage des plats effectué toutes les heures pendant la marée haute a servi à évaluer le dépôt global de carbone organique dans la couche ; à chaque marée basse successive, on a réalisé un échantillonnage pour déterminer le taux net de dépôt. La différence entre le dépôt global et le dépôt net équivaut à la remise en suspension. L'enfouissement à court terme du carbone a été quantifié par sectionnement vertical des échantillons dans les plats. Les résultats révèlent qu'à cause de la remise en suspension, le taux net de dépôt pendant 2 jours (11 $gC \cdot m^{-2} \cdot h^{-1}$) ne s'élevait qu'à 42 % du taux de dépôt global pendant une seule marée haute. La méthode est utile car elle peut apporter une solution aux flux à court terme des particules, qui peuvent être importants pour les communautés benthiques du point de vue trophique.

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The transport of sediment and associated organic matter may be an important pathway of food input to the benthos. Field observations demonstrate that meiofauna congregate near accumulations of detritus that are buried in ripple troughs (Hogue and Miller 1981). Laboratory observations indicate that feeding behavior in some benthic polychaetes is dependent on near-bed particle flux (Jumars and Nowell 1984). The trophic significance of these transport processes to benthic communities is difficult to assess because the horizontal flux of organic particles near the bed has not been measured.

Measurement of organic deposition has relied on cylindrical sediment traps that catch material falling vertically through the water column. Although such traps also collect detritus moving horizontally (Bloesch and Burns 1980), they cannot be used to measure particle dynamics close to the bed. Resuspension of bottom material into traps will confound the measurement of primary flux. The traps may also interfere with water flow and thus deposition processes (Gardner 1980). At best, these devices measure deposition to the sediment–water interface; transport during ripple migration may involve the upper few centimetres of the sediment (Grant 1981a). Various bedload traps have been used to catch sand moving along the seabed, but the efficiency of these traps is unclear (Komar 1978).

Many studies of sediment transport (see review in Nowell 1983) are not immediately applicable to biogenic particles such as fecal pellets or plant fragments, because the latter differ from similarly sized mineral grains in shape, density, and adhesive properties (Odum et al. 1979; Taghon et al. 1984). No suitable method exists to specifically measure organic deposition associated with near-bed sediment transport. In this note, I describe a "natural" sediment trap that has been used to measure deposition, resuspension, and short-term burial of organic carbon on a low-energy intertidal beach in Nova Scotia. Methodology, and results of an initial set of field experiments are presented.

Study Site

Experiments were performed during October 1981 on a sheltered sandflat in Eastern Passage, Halifax Harbour, N.S. (63°30′W, 44°37′N). Tidal range is 1.0–1.5 m. Water temperature during experiments was 14°C and salinity 29. The mean grain size of these sediments was 212 μm with 0.5–3.0% silt (<53 μm) (Van Raalte 1978). The redox potential discontinuity was sharply defined by black reducing sediments at 1–2 cm depth.

A high intertidal site was chosen for experiments because sediments could be sampled at high water by wading. Sinuous symmetrical sand ripples (wave-induced sensu Harms 1969) were usually present, but faunal burrows and tubes were scarce in the upper intertidal. A paucity of obvious bioturbation was desirable because the method was intended to emphasize physical transport of organic matter. Microscopic examination of the sediment revealed abundant organic–mineral aggregates. Macrophyte growth on adjacent hard substrate areas contributed to the seaweed wrack and finer detritus in the study area.

Materials and Methods

Traps consisted of natural sand that was ashed to remove organic matter and returned to the field in metal pans at low tide. As the tide covered the pans, ripples were formed; ripple migration was observed to remove the treated sand and replace it with ambient natural sediment. This experiment actually measured "colonization" of pans by ambient sand and associated organic matter entrained in the flow.

Oxidized sand was collected from the study site and washed in the laboratory with warm freshwater for 2 h to remove detritus, fines, and juvenile bivalves (*Mya arenaria*). The washed sediment was dried at 100°C and placed in a muffle furnace at 550°C for 4 h.

In each experiment, a row of five aluminum baking pans (20 × 20 × 4.4 cm deep) were buried at low tide with the upper rim flush to the sediment surface. Pans were then filled with organic-free sediment and wetted with filtered (0.45 μm) seawater. Sediment cores for elemental analysis were taken with a truncated 5-mL plastic syringe at the initial low tide, at hourly intervals through high tide, at the subsequent low tide, and at low tide on successive days. Single cores (to 1 cm depth; wet volume = 1 cm^3) from each of two trays were combined into a preweighed plastic scintillation vial. A replicate sample from two other pans was taken simultaneously. Identical cores were collected from ambient untreated sediments. During high tide, the pans were clearly visible and carefully approached from downcurrent to avoid disturbing the sediment. The small size of the pan coupled with the rapid influx of ambient sediment reduced any upstream–downstream gradient of carbon in the pan. Cores were taken randomly with respect to ripple microtopography and immediately stored on ice.

Sampling at successive low tides was continued until the top 1 cm of pan sediment was observed to be displaced by ambient sediment. The pink color of combusted quartz sand provided a visual tracer of displacement depth when compared with overlying ambient sediments which were tan. Sediment samples were kept frozen in the laboratory at −20°C. Vials were then dried at 60°C, acid-treated to remove carbonate material, and subsamples combusted in a Perkin-Elmer CHN Analyzer (details of method in Hargrave and Phillips 1981).

Rate definitions — The following definitions were applied to the transport of organic carbon. Gross deposition: hourly accumulation in pans within one tidal cycle (0–1 cm sediment depth); net deposition: accumulation in pans measured by sampling only at the initial and successive low tides (0–1 cm sediment depth) until an asymptotic carbon concentration occurred.

The retention of carbon by the sediment during successive low tides was consistently lower than the gross deposition that occurred within a single tidal inundation. The difference in these rates (total loss) is assumed to be due to both resuspension of carbon into the water column, and episodic burial of material below the 1-cm horizon. The rate of burial was determined by sampling the top 2 cm of sediment at initial and successive low tides, and measuring accumulation of carbon in the 1–2 cm layer. Burial subtracted from total loss is the rate of resuspension. Burial and resuspension were not distinguished in initial experiments because only the top 1 cm was sampled. Reported herein is total loss (gross minus net deposition).

Results

Results are presented for one set of pans sampled within a tidal cycle, and on successive low tides. During the initial tidal cycle, wind speeds of 15–30 km·h^{-1} (Environment Canada 1981) produced waves of 6–8 cm amplitude and 1.3–2.0 m wavelength. Ripples of 4 cm wavelength formed in pans within 0.5 h of water immersion. After tidal exposure, pink-colored sand was visible at the sediment surface in some of the pans. Pan bedforms were symetrical wave-induced ripples (8–9 cm wavelength, 0.5–1.0 cm amplitude) (Harms 1969). They were identical to and continuous with those in the surrounding sediment (Fig. 1A). Even under stronger tidal currents encountered in other experiments, ripple migration was not impeded by the pans (Fig. 1B). After emergence, pink sand in the top 1 cm was diluted by ambient sand; pure pink sand was only observed below a depth of 1.5 cm. Twenty-four hours later, the pink sand horizon was at a depth of 2.0 cm.

At the start of the experiment, ashed sediments had an order of magnitude less organic carbon than untreated ambient sediments (Fig. 2). Organic carbon accumulated in the pans exponentially, reaching an asymptote as the water ebbed. After a single high tide, carbon added through gross deposition was more than one half of that in the ambient sediment at low tide. An asymptotic carbon concentration in pans during the ebb stage of the tidal cycle indicated either that transport was minimal or that deposition and resuspension events (between hourly samples) were balanced during that period. Input of carbon during a high tide need not always follow an exponential curve; gross deposition was linear in other experiments at Eastern Passage (unpubl. data).

Carbon in ambient sediments (Fig. 2) was highly variable and differed significantly during the tidal cycle (one-way analysis of variance, $p < 0.05$), although ambient low-tide values at the start and end of the experiment were virtually identical. In both ambient and tray sediments, the greatest variability between replicate points occurred at the time of slack high tide. A patchy distribution of material settling to the sediment surface at slack water may have contributed to this variability.

In pan samples from successive low tides (Fig. 3), organic carbon again increased exponentially, approaching the levels of ambient carbon in four low tides (2 d). Net deposition curves should always become asymptotic, because carbon in the top 1 cm of the pans will eventually equilibrate with the ambient sediment. Ambient carbon was relatively stable over this period at 7–8 mg·g sediment^{-1}. Sampling ended after 2 d because pans were vandalized.

Due to the nonlinear accumulation of carbon in the pans, rates of gross and net deposition were calculated according to an exponential model:

$$(1)\quad \Delta C = C_m - C_t = C_m e^{-\alpha t}.$$

where ΔC = difference in sediment carbon in the pans between C_m (asymptotic carbon concentration (milligrams per gram)) and C_t (carbon concentration at time t), C_m is visually estimated from the curve in Fig. 2 and 3 such that $C_m - C_t > 0$, and α is the rate constant (time)$^{-1}$. In differential form:

$$(2)\quad \frac{d}{dt}(\Delta C) = -\alpha C_m e^{-\alpha t}.$$

At $t_0 = 0$:

$$(3)\quad \frac{d}{dt}(\Delta C) = -\alpha C_m$$

Dividing Equation 1 through by C_m and taking the natural logarithm of both sides yields

$$(4)\quad \ln\left(\frac{\Delta C}{C_m}\right) = -\alpha t$$

where α is the slope of the linear regression derived from a semilog plot of Equation 4. In calculations from both Fig. 2 and 3, this slope was significantly different from zero ($p < 0.05$, $r = 0.5$ and 0.9, respectively), although variability of carbon in the pans during ebb tide (Fig. 2) produced scatter in the regression for α_{gross}.

Gross deposition is the advection of organic carbon as defined by hourly time scales. The rate was not sustained over longer periods because it was counteracted by resuspension. The result is the smooth curve of net deposition seen in Fig. 3. Gross and net deposition can be compared when expressed on a time scale of (hours of water cover)$^{-1}$. If dry sediment bulk density is 1.39 g·cm^{-3}, rates in the top 1 cm calculated from Fig. 2 and 3 and Equation 3 are as follows (grams carbon per square metre per hour):

Gross deposition = 26

Net deposition = 11

Loss (resuspension and burial) = 15 (58% of gross deposition).

Material was therefore lost from the pans 58% as fast as it was deposited. Resuspension on tidal flats is often enhanced in the shallow water of early flood and late ebb (Anderson 1972; Baillie and Welsh 1980). At Eastern Passage, suspended sediments reached a maximum in the late ebb of Fig. 2 (unpubl. data), providing evidence for the resuspension of gross deposition. In spite of resuspension, the level of net deposition signified a considerable sedimentation of organic carbon at Eastern Passage. This may have been reflected in the increased sediment height in the pans that I occasionally observed. Alternating erosion and deposition of sediment are expected on

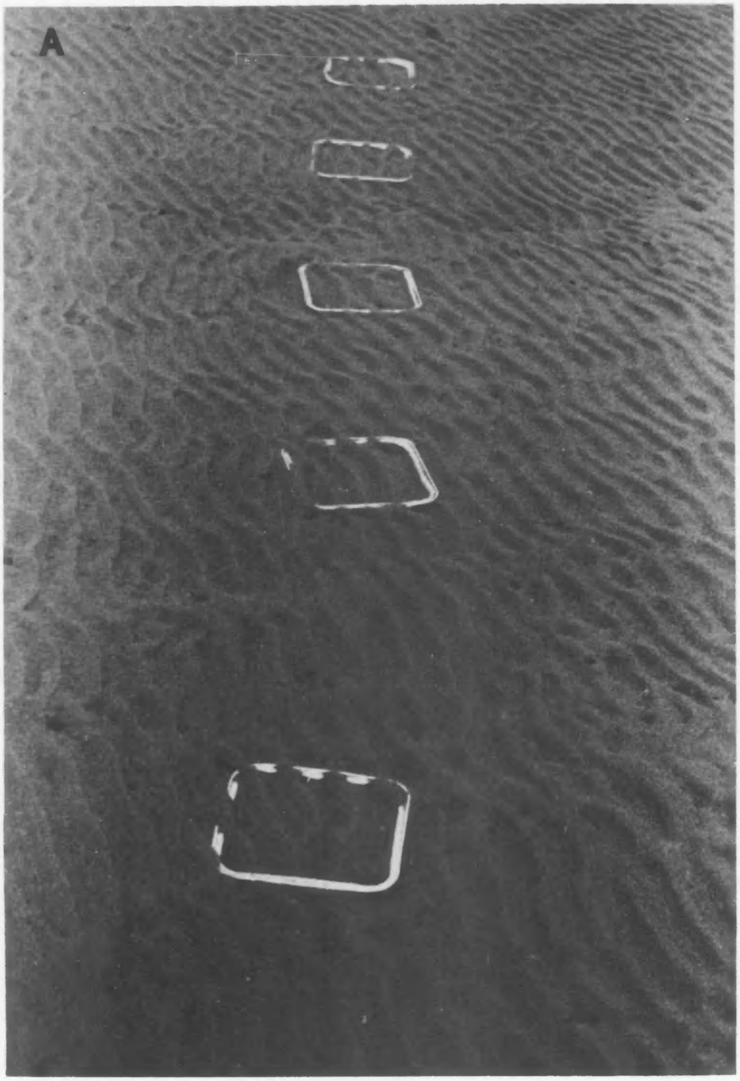

FIG. 1. Bedforms at low tide at the study site. All pans were 20 cm on a side. Note that bedforms in pans had identical dimensions to those in ambient sediments. (A) Ripples resulting after a single high tide. Continuity of the sinuous wave-induced ripples is evident between the pans and surrounding sand. (B) A single pan from later experiments after surface treated sand had been replaced with ambient natural sand. Ripples in this case indicate combined wave- and tidally-influenced flow.

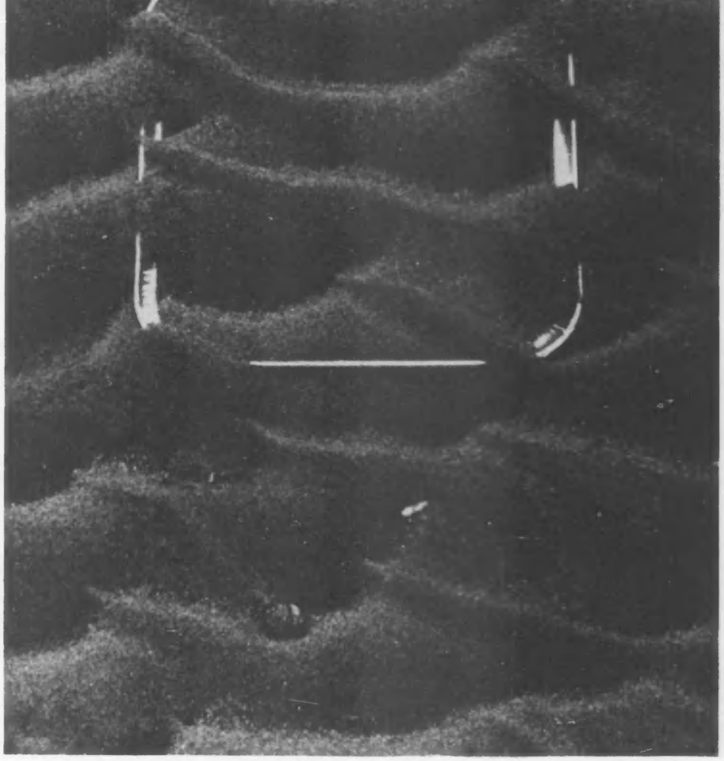

FIG. 1. (*Concluded*)

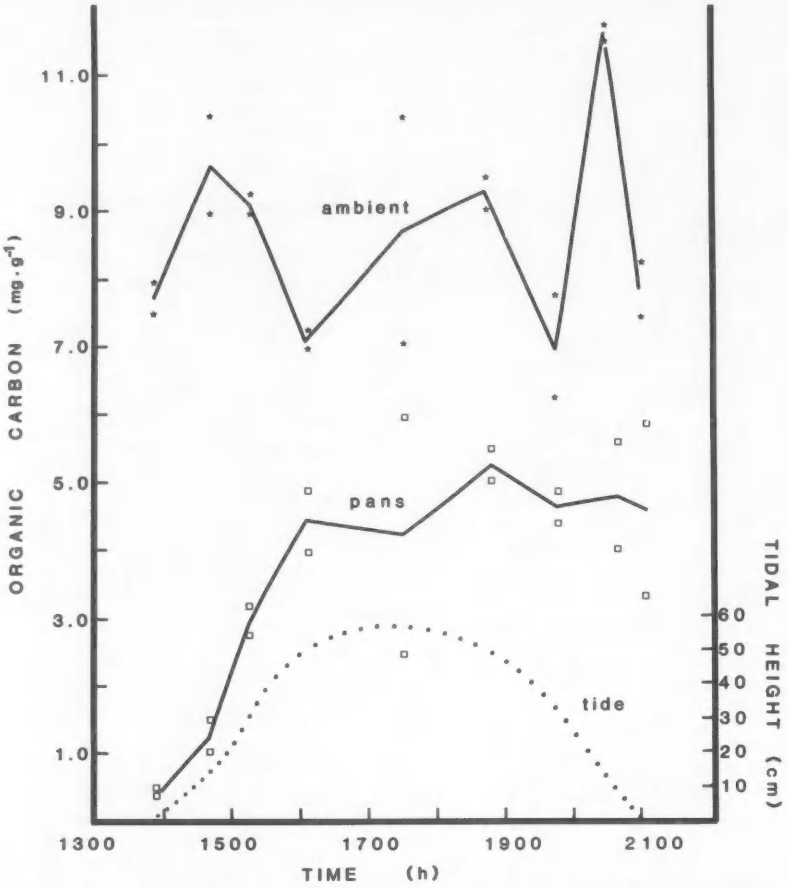

FIG. 2. Gross deposition: fluctuations in organic carbon in pans (□) and ambient sediments (★) during a single high tide (···). Lines connect the means of the two replicate points. The pans initially contained only ashed sediment and filtered seawater.

intertidal sandflats (Pickrill 1979; Carling 1982), although little is known about how carbon transport relates to bulk sediment transport.

Discussion

This method provides a simple and inexpensive means to examine detrital dynamics on sand substrates. Where only net deposition is of interest, one could emplace pans of clean sediment and sample only at successive low tides. Visual inspection of sediment coloration shows roughly when the top 1 cm of sediment has been replaced with ambient sediment. New pans may be deployed at intervals to provide a record of organic matter movement over a given period. The pans could also be deployed subtidally if they were filled prior to emplacement and fitted with lids.

Like the natural sediment surface, the pans will accumulate material both settling from suspension and moving as bedload. In terms of food input to the benthos, this is desirable because the method is not biased toward one mode of deposition. However, freshly sedimented detritus (e.g. phytoplankton) cannot be distinguished from "old" organic matter which is advected from areas adjacent to the pans. Due to varying organic quality, it may be useful to distinguish fluxes of the most labile portions of total organic carbon (e.g. microbial numbers, ATP, chlorophyll). Live organisms such as meiofauna probably occupied the pans, but no macrofauna or their traces were observed. The method integrates all advective processes, and no attempt was made to separate physical transport from potential bioturbation effects.

Bloesch and Burns (1980) considered tray sediment traps to be ineffective due to "unhindered resuspension." Håkanson (1976) successfully used tray-like traps in a Swedish Lake, but suggested they only be deployed on quiet bottoms where fine particles settle. Reynolds and Godfrey (1983) placed boxes of glass beads above a silty lake bottom, but found that the interstices of surface sediment were rapidly saturated and subsequent deposition was easily resuspended. The above experiments, however, were intended to measure vertical deposition and not bedload transport.

One potential problem with my method is that cleansing and ashing of the sediment changed its transport properties. For example, the binding action of microbial films in natural sediments may inhibit transport (deBoer 1981; Grant et al. 1982). In my study, ripple dimensions were identical in pan and

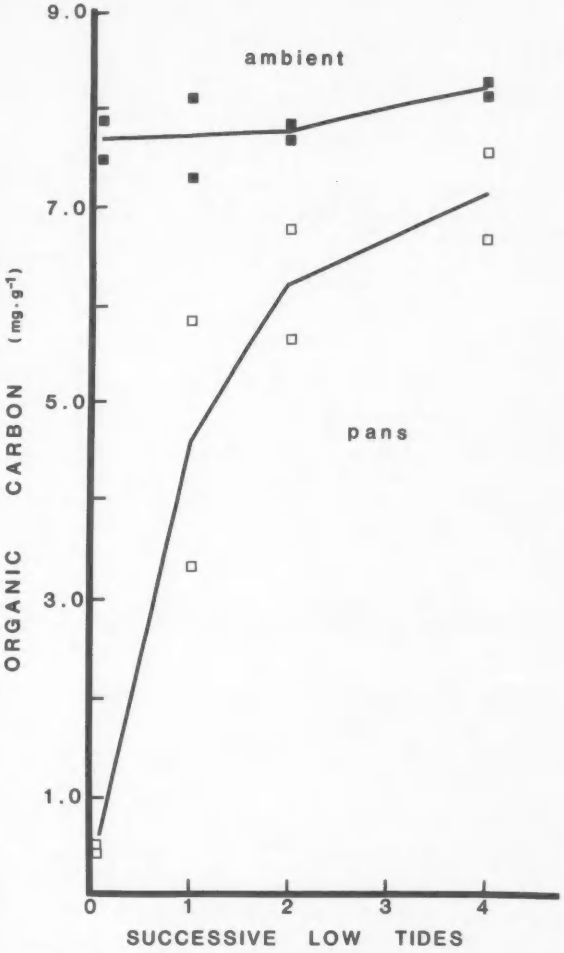

FIG. 3. Net deposition: fluctuations in organic carbon in pans (☐) and ambient sediments (■) based on samples at successive low tides. Lines connect the means of the two replicate samples. The first points for the pans represent their initial placement.

ambient sediments; this suggests that both sediments were responding to transport in the same way. In addition, the presence of pans in the intertidal zone did not produce local sedimentation artifacts such as scour or accretion.

A second potential problem is that microbial growth in situ could supplement carbon brought by advection. In natural sediments, the standing stock of bacterial carbon is often only a small percentage of total organic carbon (Cammen 1982). Microalgal carbon at Eastern Passage (calculated from chlorophyll levels in ambient sediments) also contributed little to bulk carbon levels (Van Raalte 1978; J. Grant, unpubl.). Moreover, rates of detrital advection are generally much greater than in situ microbial production. For example, in recent studies of New York Bight, the growth of bacterial cells in cylindrical sediment traps was unimportant relative to the vertical flux of bacteria into the traps (Ducklow et al. 1982). Measurements at Eastern Passage demonstrate that benthic primary production and respiration are minor relative to bulk carbon flux (Hargrave and Phillips 1981; J. Grant, unpubl.).

My results indicate that the horizontal transport of organic carbon is extremely rapid. In contrast, vertical sedimentation of particulate organic carbon in oceans and bays is three orders of magnitude less (Valiela 1984). I know of no measurements similar to mine, but a previous estimate of bulk sediment transport provides a rough comparison. Based on flume studies of ripple migration and field measurements of tidal current velocities, I have investigated sediment transport on an intertidal sandflat in South Carolina (Grant 1983). Grain size and bulk density were similar to that at Eastern Passage; total organic content was about 0.5% by weight (Grant 1981b and unpubl. data). In the mid-intertidal, the rate of transport was 6.1×10^3 cm^3 sediment moved · m^{-2} sediment surface · (h ebb flow)$^{-1}$. If roughly one half of the organic content was carbon, the resulting rate of carbon transport would be 21 $g\,C \cdot m^{-2} \cdot h^{-1}$. This comparison between two different tidal flats is somewhat arbitrary, and assumes a simple relationship between the movement of bulk sediment and carbon, but it suggests that sediment transport during non-storm conditions can reasonably result in carbon transport on the order of 10 $g\,C \cdot m^{-2} \cdot h^{-1}$.

Rates of gross deposition are unique to the current and wave conditions of a single tidal cycle. Under calmer conditions, pink sand remained on the surface of pans for a number of days (unpubl. data). Further experiments at Eastern Passage will clarify the variation in the shape of deposition curves over a variety of wind and current conditions. It is not my intention to construct a yearly budget of organic deposition and resuspension. My measurements are scaled to biotic processes (e.g. utilization of organic matter by benthic organisms), which I have also measured on an hourly basis. An important result of the pan experiments is that short-term sampling (hourly) is necessary to resolve the rates at which organic matter reaches intertidal benthos. The top 1 cm of sediment undergoes a huge flux of organic matter and a highly variable carbon content due to horizontal advection during high tide. Benthic organisms respond rapidly to changes in near-bottom food supplies (Jumars and Nowell 1984). The quality and quantity of the material involved in these fluxes may thus be important in the trophic dynamics of benthic communities. The pan method provides a means to measure these transport processes.

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El Niño Events and Variability in a Pacific Mackerel (*Scomber japonicus*) Survival Index: Support for Hjort's Second Hypothesis

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From 1928 to 1965 the higher survival rates to age 1 for Pacific mackerel (*Scomber japonicus*) in the California Current occurred during years of decreased southward transport (as indicated by sea level), which in turn is related to El Niño events. During such years, plankton biomass was relatively low. Conversely, Pacific mackerel survival rates to age 1 were low during periods of increased southward transport, when plankton biomass was high. We conclude that survival rates during the early life history may be more influenced by hydrographic processes in a direct manner than by biological interactions. This interpretation is consistent with Hjort's (1914. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 20: 1–228) second hypothesis to explain interannual variability in recruitment to fish populations.

De 1928 à 1965, les taux élevés de survie du maquereau (*Scomber japonicus*) jusqu'à l'âge d'un an dans le courant de Californie ont coïncidé avec les années de faible transport vers le sud (comme l'indiquent les niveaux de la mer) qui, à son tour, était lié à El Niño. Pendant ces années, la biomasse planctonique était relativement peu élevée. Inversement, les taux de survie du maquereau jusqu'à 1 an étaient faibles pendant les périodes de transport élevé vers le sud quand la biomasse planctonique était importante. Les auteurs formulent la conclusion que les taux de survie au début du cycle vital sont peut-être plus directement touchés par les processus hydrographiques que par les interactions biologiques. Cette interprétation s'accorde avec la seconde hypothèse de Hjort (1914. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 20 : 1–228) pour expliquer la variabilité interannuelle du recrutement dans les populations de poisson.

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Hjort (1914, p. 203) generalized that year-class size is determined early in the life history, prior to recruitment to the fishery. He went further to say that the most critical period during which year-class size is determined probably occurs during the "very earliest larval and young fry stages." Hjort (1914) hypothesized that two factors could be involved in the rate of decline in larval numbers: nourishment of the larvae and variable drift of the larvae and young fry with the currents. In discussing the first hypothesis, Hjort wrote (1914, p. 205):

> If the time when the eggs of the fish are spawned, and the time of occurrence of this plant growth both be variable, it is hardly likely that both would always correspond in point of time and manner. It may well be imagined, for instance, that a certain ... lapse of time might occur between the period when the young larvae first require extraneous nourishment, and the period when such nourishment is first available. If so, it is highly probable that an enormous mortality would result.

Regarding the drift of larvae and young fry with the currents, Hjort wrote (1914, p. 206):

> It is possible that many individuals perish during such drifting movements: nothing is, however, definitely known as to this. It would be especially desirable to ascertain the extent of such movement, and how far the young fry are able to return, of their own volition, to such localities as offer favourable conditions for their further growth.

He was not more specific with respect to the effect of interannual differences in advection within the larval distributional area on variable larval and post-larval survival. He did, however, recognize that advection could transport larvae to an inappropriate geographic location. We interpret his second hypothesis in this more limited sense: the differential loss of larvae from the appropriate larval distributional area due to interannual differences in advection. Both hypotheses (nourishment and drift) were given equal weight, and interrelationships between them were recognized. Clearly, Hjort's recognition of the importance of the cooccurrence of fish larvae with their prey, his first hypothesis, laid the foundation for the match–mismatch theory of Cushing (1975). It is not well recognized in the subsequent literature on recruitment variability that Hjort defined a second hypothesis.

Developments since Hjort (1914) have stressed the importance of food availability during the larval phase (Cushing 1975; Jones 1973; Lasker 1975, 1978; Lawrence 1977) rather than advective losses. The match–mismatch theory of Cushing (1975) explicitly links recruitment variability to interannual differences in the timing of phytoplankton blooms and subsequent generation of copepod nauplii broods. Where year-class sizes or lagged catches have been related to physical oceanographic measures, the observed variability has most frequently been interpreted in relation to larval food (physical events lead to more or less "available" plankton which results in variable larval survival) (Barber and Chavez 1983; Sutcliffe 1972, 1973; Sutcliffe et al. 1983).

Several recent workers, however, have stressed the direct role of physical processes both in generating recruitment variability and on the definition of population structure. Bailey (1981) and Nelson et al. (1977), for example, have interpreted year-class variability of, respectively, Pacific hake (*Merluccius productus*) and Atlantic menhaden (*Brevoortia tyrannus*) as being caused by interannual differences in advective losses at the larval phase. Bailey (1981) did, however, discuss the interaction between offshore transport of hake larvae and their feeding environment. Iles and Sinclair (1982) and Sinclair and Tremblay (1984) have argued that the match–mismatch theory (Cushing 1975) is not supported by observations on the primary production cycle in the larval distributional areas of Atlantic herring (*Clupea harengus harengus*) populations. Quite simply the larval distributional areas of many herring populations are not characterized by predictable seasonal phytoplankton blooms in relation to the timing of spawning. It is argued that there should be a decoupling between the explanations of recruitment variability and the timing of spawning. In sum, the existence of Atlantic herring populations, their mean size, and their timing and location of spawning are hypothesized to be linked to physics rather than to seasonal changes in the planktonic food of larvae.

Bernal (1981), Bernal and McGowan (1981), and Chelton et al. (1982) have interpreted the large-scale interannual physical and biological interactions in the California Current. They note that the physical and biological properties are dominated by a large-scale interannual signal. Zooplankton abundance was shown to be primarily influenced by large-scale variations in the flow of the California Current, higher biomasses being associated with increased southward transport. Somewhat surprisingly, on the large spatial and temporal scales considered, zooplankton abundance was unrelated to wind-driven coastal upwelling. Much of the variability in the transport and in zooplankton abundance was related to El Niño phenomena. In these studies, linkages with recruitment to fish populations in the California Current system were not addressed. Parrish and MacCall (1978) had earlier evaluated relationships between Pacific mackerel (*Scomber japonicus*) recruitment and climatic variation, giving particular attention to wind-driven transport indices. Since plankton biomass indices were not available to Parrish and MacCall, and the importance of El Niño events on the oceanography of the California Current was not yet fully appreciated, we believe that a reevaluation of recruitment mechanisms for this species is warranted.

In this note the extensive obsevations published in the literature on the oceanography of the California Current system and on the relative survival of Pacific mackerel are brought together. The relationships that emerge are evaluated in light of the two hypotheses that Hjort (1914) proposed to explain interannual variability in recruitment to fish populations.

Data Sources and Constraints

The California Current ecosystem has been monitored perhaps more extensively than any other in the world's oceans, both for the fish populations and the oceanographic features. Much of the data have been synthesized in several recent publications (Bernal and McGowan 1981; Chelton et al. 1982; Smith and Eppley 1982). The data used in this analysis are listed in Table 1.

The index of survival for Pacific mackerel is year-class size at age 1 divided by spawning biomass, and is derived from table 14 of Parrish and MacCall (1978). The most recent years of the sequential population analysis (1966–68) are not used here, since the estimates of year-class strengths and of spawning biomass for this part of the population matrix are heavily dependent on the input values of the source analysis (Pope 1972). The index is at least partially corrected for density-dependent changes in egg production in that Parrish and MacCall have used a variable maturity ogive in estimating the

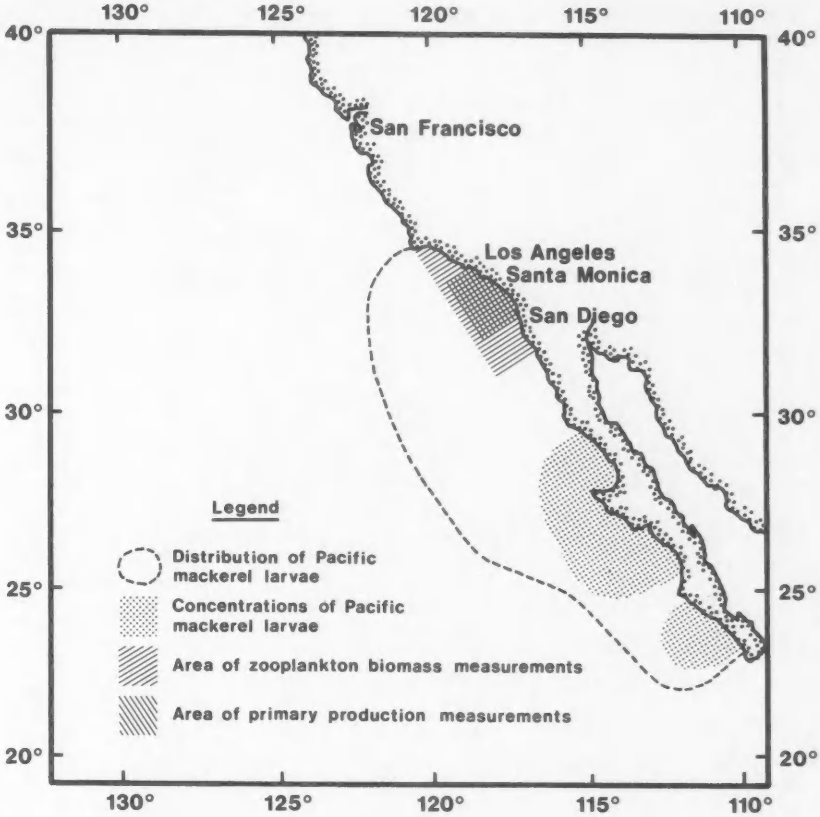
TABLE 1. Southern California Bight data used in analysis. Mean primary production ($C \cdot m^{-2} \cdot d^{-1}$) and zooplankton biomass ($g \cdot m^{-2}$) values from Smith and Eppley (1982). Pacific mackerel survival index (SI) (biomass at age 1/biomass spawners) from Parrish and MacCall (1978, table 14). Sea level data from Chelton et al. (1982, fig. 12). PP = primary production; Zoop = zooplankton biomass (550-μm mesh); MP = microplankton (64-μm mesh).

Year	Mackerel SI	Sea level	Mar. PP	June PP	Sept. PP	Dec. PP	Mar. Zoop	June Zoop	Sept. Zoop	Dec. Zoop	Annual MP
1928	0.523	−1.51	0.315	0.540	0.503	0.244	—	—	—	—	—
1929	0.808	−1.48	0.460	0.424	0.276	0.165	—	—	—	—	—
1930	0.858	0.55	0.250	0.559	0.315	0.132	—	—	—	—	—
1931	0.921	1.81	0.142	0.227	0.219	0.254	—	—	—	—	—
1932	0.513	−0.21	0.383	0.616	0.556	0.278	—	—	—	—	—
1933	0.133	−2.89	0.485	0.922	0.673	0.299	—	—	—	—	—
1934	0.059	−3.26	0.230	0.367	0.334	0.178	—	—	—	—	—
1935	0.081	−1.27	0.409	0.488	0.407	0.251	—	—	—	—	—
1936	0.268	−0.96	0.334	0.384	0.239	0.178	—	—	—	—	—
1937	0.308	−0.16	0.412	0.424	0.332	0.168	—	—	—	—	—
1938	0.610	0.16	0.329	0.692	0.368	0.272	—	—	—	—	—
1939	0.603	−1.70	0.501	0.533	0.291	0.100	—	—	—	—	—
1940	0.604	2.51	0.238	0.576	0.352	0.157	—	—	—	—	—
1941	1.202	5.67	0.168	0.526	0.384	0.164	—	—	—	—	—
1942	0.571	3.74	0.352	0.536	0.351	0.200	—	—	—	—	—
1943	0.327	0.82	0.293	0.685	0.335	0.186	—	—	—	—	—
1944	0.320	−0.15	0.347	0.796	0.454	0.215	—	—	—	—	—
1945	0.152	−1.16	0.489	0.617	0.285	0.299	—	—	—	—	—
1946	0.201	−0.23	0.397	0.421	0.346	0.264	—	—	—	—	—
1947	2.311	0.16	0.314	0.490	0.357	0.268	—	—	—	—	—
1948	1.408	−0.95	0.463	0.781	0.473	0.340	—	—	—	—	—
1949	0.105	−1.85	0.515	0.837	0.352	0.294	—	—	—	—	—
1950	0.038	−2.18	0.399	0.681	0.450	0.235	—	—	—	—	—
1951	0.050	0.21	0.356	0.553	0.490	0.215	15.22	21.16	7.00	8.52	29
1952	1.949	2.12	0.403	0.774	0.456	0.251	12.63	20.40	17.50	10.50	35
1953	4.416	0.68	0.458	0.710	0.481	0.244	16.59	66.51	31.05	6.54	78
1954	0.865	−0.16	0.359	0.502	0.413	0.229	10.96	32.12	9.13	7.61	39
1955	0.781	−1.99	0.457	0.656	0.315	0.317	11.26	24.51	13.09	13.39	37
1956	0.212	−2.25	0.482	0.685	0.362	0.204	17.35	42.31	22.83	22.69	78
1957	0.286	1.53	0.315	0.456	0.336	0.130	16.59	14.16	5.63	4.57	31
1958	2.239	5.00	0.193	0.587	0.278	0.115	7.00	11.26	2.44	3.28	18
1959	1.091	4.96	0.193	0.304	0.233	0.154	5.02	8.52	7.30	5.78	18
1960	1.594	0.89	0.334	0.656	0.456	0.216	13.09	20.09	9.74	3.65	28
1961	0.897	−0.81	0.304	0.680	0.479	0.301	14.61	44.60	6.85	9.89	43
1962	0.086	−0.53	0.407	0.911	0.429	0.230	26.03	100.76	24.20	8.07	98
1963	0.052	0.63	0.338	0.652	0.323	0.159	21.46	71.99	7.31	15.68	67
1964	0.020	−2.01	0.339	0.920	0.356	0.352	28.77	37.14	42.01	15.37	76
1965	0.106	0.21	0.348	0.890	0.392	0.194	10.05	20.09	17.50	7.46	39

annual mature biomass. However, it is implicitly assumed that the fecundity – fish weight ratio does not vary significantly. A low variability in this ratio is characteristic of pelagic species in general (Ware 1980).

Sea level, which is used as an index of changes in the transport of the California Current, is from Chelton et al. (1982). Single sea level values for each year from 1928 to 1965 were obtained by taking the beginning-of-the-year values from their fig. 12. Chelton et al. (1982) showed that the relationship between coastal tide records and geostrophic flow is very strong, high sea level corresponding to reduced southward flow or anomalous northward flow, and low sea level signalling above-normal southward flow. They further demonstrated that the strength of the California Current is rather closely related to El Niño occurrences in the eastern tropical Pacific. El Niño is associated with positive sea level anomalies which correspond to reduced southward flow or anomalous northward flow. Negative El Niño events are associated with low California sea level and anomalous southward flow. Limitations on the use of sea level as an index of large-scale physical and biological variability were discussed by Chelton et al. (1982).

The time series on primary production and zooplankton biomass are taken from Smith and Eppley (1982). The estimates of quarterly primary production are for the Southern California Bight (Fig. 1), and are derived from a regression based on primary production measurements (1974–79), Scripps pier temperature anomalies, and day lengths (Smith and Eppley 1982, table 2). The Southern California Bight quarterly zooplankton biomass estimates were recalculated from Longhurst et al. (1972) by Smith and Eppley (1982, table 3). The biomass time series for a 64-μm-net microplankton from Santa Monica Bay was taken from Smith and Eppley (1982, table 4). Smith and Eppley (1982) and our Table 2 show a close relationship between microplankton biomass collected by the 64-μm-mesh net in Santa Monica Bay and the zooplankton biomass retained by the CalCOFI 550-μm-mesh net for the Southern California Bight. This suggests that the more complete zooplankton biomass time series can be used as a measure of microplankton


130°
125°
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San Francisco
Los Angeles
Santa Monica
San Diego
Legend
Distribution of Pacific mackerel larvae
Concentrations of Pacific mackerel larvae
Area of zooplankton biomass measurements
Area of primary production measurements

FIG. 1. California coast showing distribution of Pacific mackerel larvae (after Kramer 1960) and areas where phytoplankton and zooplankton measurements were obtained.

TABLE 2. Rank correlations between variables listed in Table 1. $N = 38$ for all pairwise tests except those involving zooplankton and microplankton ($N = 15$). $^{**}p < 0.01$; $^{*}p \leq 0.05$.

	Sea level	Mar. PP	June PP	Sept. PP	Dec. PP	Mar. Zoop	June Zoop	Sept. Zoop	Dec. Zoop	Annual MP
Mackerel SI	0.53**	−0.28*	−0.16	−0.03	−0.07	−0.56*	−0.33	−0.16	−0.55*	−0.37
Sea level		−0.58**	−0.20	−0.13	−0.44**	−0.50*	−0.64**	−0.49*	−0.72**	−0.69**
Mar. PP			0.38*	0.22	0.37*	0.36	0.55*	0.74**	0.51*	0.63**
June PP				0.54**	0.44**	0.46*	0.51*	0.78**	0.40	0.67**
Sept. PP					0.46**	0.26	0.39	0.23	0.04	0.28
Dec. PP						0.31	0.52*	0.63**	0.49*	0.47*
Mar. Zoop							0.73**	0.47*	0.52*	0.72**
June Zoop								0.52*	0.63**	0.90**
Sept. Zoop									0.45*	0.69**
Dec. Zoop										0.59*

(e.g. phytoplankton and small zooplankton), which includes the major dietary components of many marine larval fish (Last 1980). Hunter and Kimbrell (1980) reported that the major prey items of Pacific mackerel larvae were copepod stages, cladocerans, oikopleurans, gastropods, eggs, and diatoms. A similar diet is found in Atlantic mackerel (*Scomber scombrus*), with phytoplankton a prevalent food source in the smaller larvae (Peterson and Ausubel 1984).

The geographical area of the plankton time series (Southern California Bight) is not coincident with the overall distributional range of Pacific mackerel larvae. The larval distributional area for Pacific mackerel is the California Current from Point Conception to the tip of Baja California (Fig. 1). The Southern California Bight is at the northern part of the larval distributional range. Chelton et al. (1982) have, however, shown a high degree of coherence between zooplankton volume estimates in the different parts of the CalCOFI sampling grid (San Francisco to Baja California). Thus, although the plankton data used in the

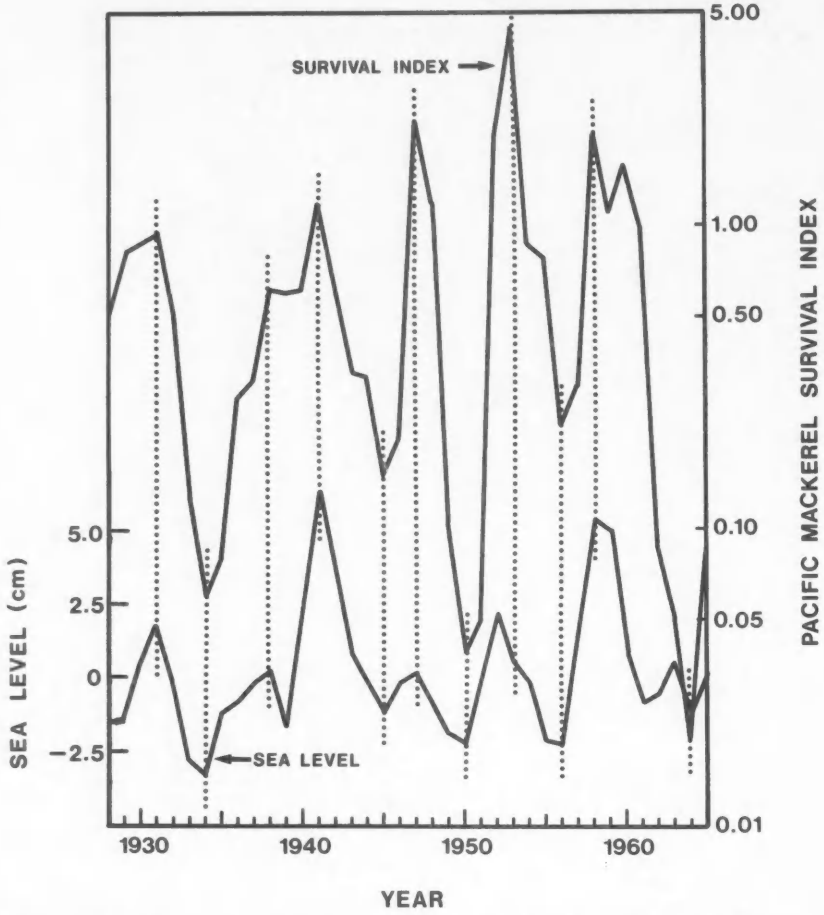

FIG. 2. Fluctuations in Pacific mackerel survival index and sea level (January) from 1928 to 1965. Sea level (double 13 mo running mean) averaged over San Francisco, Los Angeles, and San Diego (from Chelton et al. 1982, fig. 12).

analysis do not cover the full distributional range of the mackerel larvae, they should be representative. Pacific mackerel larvae occur over a relatively broad area and time period: most are found from April through July off southern California, and March through August off Baja California (Kramer 1960). Thus, the larval phase could be considered to span the spring to summer period.

Results

There is essentially a one-to-one relationship between the interannual variability in survival of Pacific mackerel to age 1 and the sea level index (Fig. 2). Good survival is associated with high sea level (i.e. reduced southward flow of the California Current). Poor survival is associated with strong southward flow. Thus, El Niño associated events (reduced southward flow of the California Current) generate conditions that are good for the survival of Pacific mackerel.

Patterns among the biological and physical variables (Table 2) are clear. Mackerel survival is positively correlated with the sea level index (as observed in Fig. 2), but is negatively correlated with all of the plankton estimates. Even though the significance levels are low, the sign relationship is consistently negative. As already reported by Smith and Eppley (1982) and Chelton et al. (1982), the phytoplankton and zooplankton parameters behave coherently over large space and time scales. The phytoplankton production and zooplankton biomass estimates are positively related to the strength of the California Current (i.e. negatively related to sea level).

For this unique study area where the complex interrelationships between the physical oceanography and the plankton dynamics at the interannual time scale have been thoroughly analyzed (Bernal 1980; Chelton 1980; Chelton et al. 1982), fish survival to age 1 for one species is not positively correlated with food availability as estimated by zooplankton volume. It does, however, parallel in a remarkable fashion (from 1928 to 1965) advection differences driven by the sequence of El Niño events.

Discussion

What is the significance of these results? High survival rates to age 1 were observed during El Niño events. During the high-survival years the southward transport of the California Current was reduced. Also during such years plankton biomass was relatively low. Conversely, during negative El Niño years survival rates to age 1 were low, transport of the California Current was more rapid, and plankton biomass was relatively high. Also, survival rate was negatively correlated with initial egg and larval abundances (as indicated by spawning biomass) over the range of 30 000 to 600 000 t (see fig. 12 of Parrish and MacCall 1978).

There are several possible interpretations of this set of observations — interpretations that could highlight the role of food availability, predation, or the direct role of physical processes. Low zooplankton biomass as estimated here during high-survival years does not necessarily lead to the conclusion that food is of secondary importance. Zooplankton biomass in the larval distributional area may not reflect the appropriate size and quality of food required for high survival rates, but note that the more offshore zooplankton volume estimate is highly correlated with microplankton biomass (a more reliable index of larval food) in a coastal embayment. To buttress the food availability argument one has to make inferences from information that is unavailable and unlikely to become available in the context of this historical data set.

Lasker (1975, 1978) has argued that it is not the overall larval food biomass or production that is critical to larval survival but its distribution in space, or its patchiness. If the variance in plankton biomass (or its patchiness) increases in relation to the mean, the results presented here are not consistent with the Lasker "stability-food patchiness" hypothesis.

Another interpretation is that "effective" survival rates are physically controlled in a direct sense. By effective survival we mean those egg/larvae/post-larvae that actually recruit to the mackerel population. Egg/larval/post-larval mortality as such is therefore not implicit in this interpretation. Larvae that are transported or dispersed out of the population's larval distributional area (or "retention" area) may not actually die, but perhaps do not become members of the juvenile/adult migrating population subsequent to metamorphosis. The proportion of eggs/larvae/post-larvae that are retained within the distributional area shown in Fig. 1 should be, at least partially, a function of the strength of the California Current itself. The strength of the rank correlation ($r = 0.53$) between survival rates to age 1 and sea level (or El Niño events) is not in itself very convincing, but the obvious coherence between the two time series over 38 yr is striking. It may well be that in nature a tight causal relationship between advection and effective survival rate actually exists, but that the indirect signals of the events in Fig. 2 are noisy. Sea level after all only estimates the relative transport of the California Current and the strength of the El Niño event. Cohort analysis only estimates actual recruitment at age 1 and mature biomass. Direct physical control of the effective survival of eggs, larvae, and post-larvae to the self-reproducing Pacific mackerel population may well account for much of the interannual variability. In this interpretation the existence of an appropriate geographical area for the larval stage in relation to the life cycle as a whole is stressed. Where the larvae are located in geographic space may be as important as their feeding environment.

Parrish and MacCall (1978), in a comprehensive treatment of Pacific mackerel recruitment, considered the importance of combinations of 12 environmental variables and five spawner–recruit functions. Several combinations of physical variables, spawner–recruit functions, and time periods accounted for significant portions of the Pacific mackerel year-class strength or survival index variability. Two different sea level indices (monthly sea level at La Jolla and sea level differences between San Francisco and Hilo, Hawaii) were used, both of which were different than that used here. The sea level index used in the present study has been shown by Chelton et al. (1982) to be a good indicator of large-scale changes in the California Current system. The results of the simple analysis presented here are not necessarily at odds with Parrish's and MacCall's (1978) more comprehensive analysis because of the intercorrelations among some of the variables used in the present study and that of Parrish and MacCall (1978). The sea level index used here was not examined by Parrish and MacCall (1978), however, and our analysis is open to a different interpretation because of the greater understanding of large-scale oceanographic processes in the California Current that resulted from the work of Bernal (1980) and Chelton (1980) (as summarized in Chelton et al. 1982).

From the data sets on hand (as extensive as they are), a food or advection hypothesis cannot be ruled out, yet a simple interpretation that is fully consistent with all the observations on hand is the second of the two hypotheses that Hjort (1914) proposed to explain variability in recruitment. Such an interpretation is also consistent with recent hypotheses on fisheries population biology that stress the importance in a direct sense of physical oceanographic processes (Iles and Sinclair 1982; Nelson et al. 1977; O'Boyle et al. 1984; Sinclair and Tremblay 1984).

This interpretation (importance of physics over biological interactions) is in addition consistent with several other observations on the fisheries biology of the California Current system. Bernal and McGowan (1981) described a tight relationship between temperature, salinity, nutrients, and phytoplankton (their fig. 2, 3, 4, and 5). Fish larval distributions, however (their fig. 6 and 7), do not follow the same pattern. The larval distributions of the fish species described are not coincident with maximal food availability.

Parrish et al. (1981) have argued that the reproductive strategies of fish species in the California Current minimize larval drift and dispersion. For example, "coastal fish species having pelagic larvae tend to spawn during the winter when surface drift is generally directed toward the coast, rather than during the more productive upwelling season." Timing of spawning does not appear to be linked to the timing of seasonal plankton events — quite the opposite. Parrish et al. (1981) in fact went further and suggested what is observed here: that anomalies in advective phenomena could cause variable spawning success.

Iles (1973) interpreted the observed variability in the larval/post-larval survival index of Pacific sardine (*Sardinops caerulea*) in the California Current in relation to the Rossby wave system of high-pressure ridges which extend from the poles toward temperate latitudes. The large-scale climate – El Niño interaction has become increasingly better understood during the past few years (Rasmusson and Wallace 1983). The linking of recruitment variability (as estimated by the survival index) to large-scale climatic events by Iles (1973) is further supported by the results presented here for a different species.

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Breeding Tubercles in Three Species of *Gadus* (Cods)

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Vladykov, V. D., C. B. Renaud, and S. Laframboise. 1985. Breeding tubercles in three species of *Gadus* (cods). Can. J. Fish. Aquat. Sci. 42: 608–615.

Breeding tubercles in *Gadus* are described for the first time. Each of the three known species of *Gadus* displays specific peculiarities: in *G. ogac*, tubercles are numerous, long, and club-shaped; in *G. morhua*, tubercles are numerous, medium in length, and horn-shaped; and in *G. macrocephalus*, tubercles are few and very small. These breeding tubercles may be used for taxonomic purposes. It is probable that the tubercles may serve to maintain contact during the reproductive period.

Les tubercules nuptiaux chez *Gadus* sont décrit pour la première fois. Chacune des trois espèces connues de *Gadus* démontre des péculiarités spécifiques : chez *G. ogac*, les tubercules sont nombreux, longs et en forme de massue ; chez *G. morhua*, les tubercules sont nombreux, de longueur moyenne et en forme de corne ; et chez *G. macrocephalus*, les tubercules sont peu nombreux et très petits. Ces tubercules nuptiaux peuvent servir à des fins taxonomiques. Il est probable que ces tubercules servent à maintenir le contact pendant la période de reproduction.

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Members of the family Gadidae, especially those of the genus *Gadus*, play a very important role in marine fisheries. Yearly catches in Atlantic, Arctic, and Pacific oceans amount to several million kilograms. In spite of this abundance, many biological aspects of the *Gadus* species, especially their reproductive cycles, are not sufficiently studied. For instance, there is no published information on the presence of breeding tubercles in both males and females of Atlantic *Gadus*. Indeed, the existence of breeding tubercles in *Gadus* species was not stated in the important publications by Svetovidov (1948), Brawn (1961), Leim and Scott (1966), and Hart (1973), nor was it mentioned in Wiley and Collette's (1970) or Collette's (1977) reviews of breeding tubercles in different families of fishes.

The purpose of the present note is to compare the number and peculiarities of breeding tubercles in three species of *Gadus*. These characters may be useful for taxonomic purposes.

Material and Methods

For the present study we were able, although with difficulty, to obtain rather limited numbers of different species of *Gadus*.

Our material is represented by 20 specimens studied in detail (Tables 1–4) and another 22 studied in lesser detail (Table 1). The latter group was principally collected in the Canadian Arctic and is deposited in the National Museum of Natural Sciences, Ottawa.

Some of our specimens were not in the best condition: in several fish, patches of scales were missing and much of the skin was thickly covered by mucus. In spite of this and the presence of dark pigment, we were able to ascertain the principal differences in the number and size of tubercles.

Five samples of skin with scales (about 15 × 20 mm in size) were typically removed from the left side of the body. To replace defective samples, new samples were taken from the right side of the fish. Samples were stained with alizarin and 2% KOH and were stored in 50% ethyl alcohol. In the above specimens numerous scales (Table 2) were counted.

The position of the skin samples was as follows (Fig. 1):

Position	Definition
a	On the back in front of the 1st dorsal fin
b	Along the lateral line under the 1st dorsal fin
c	On the flank under the 2nd dorsal fin
d	On the side under the base of the pectoral fin
e	On the side above the middle of the 1st anal fin

On each sample ("square"), tuberculate scales were counted separately from scales without tubercles (Table 3). By adding both counts, the number of scales with tubercles was expressed as a percentage of the total number (Table 3). Moreover, 10 scales from each species (5 for males and 5 for females) were selected from square *a* to study the relationship between tubercle length and the length of the scale bearing it (Table 4).

Localities from which study material was obtained — We use plastic tags belonging to our laboratory for easy identification of interesting specimens.

Gadus ogac: 26 specimens, 1 (tag Y4911) from western Greenland, Sept.–Oct. 1967; 11 (without tags) from Northwest Territories, 28 Aug. 1962 and 7 Sept. 1969; 3 (tags W3561–63) from eastern Hudson Bay, 5 Sept. 1963; 2 (tags W3549, 3551) 30 July 1976, 7 (without tags) 29 Aug. 1964 – 5 Aug. 1982, both samples from Labrador; 2 (tags Y4912–13) from Miramichi Bay, 25 Feb. 1982.

Gadus morhua: 10 specimens, 3 (without tags) from Port Burwell, 13 Aug. 1967; 1 (without tag) from Kennebecasis River, New Brunswick, 4 April 1966; 2 (tags Y4915, 4917) from Miramichi Bay, 25 Feb. 1982; 4 (tags W3553, 3555, 3557, 3559) off Nova Scotia, spring 1982.

Gadus macrocephalus: 6 specimens, (tags Y4901, 4903, 4905, 4907–09) all from southwest coast of Vancouver Island, 3 Feb. 1982.

TABLE 1. *Gadus* specimens studied.

		Number of specimens			
		Studied in detail		Studied in lesser detail	
Species	TL (mm)	♂	♀	♂	♀
G. ogac Richardson 1836	249–536	4	4	6	12
G. morhua Linnaeus 1758	408–644	4	2	1	3
G. macrocephalus Tilesius 1810	525–620	3	3	—	—

TABLE 2. Number of scales studied in three species of the genus *Gadus*.

		Number of scales	
Species	Number of specimens	Range	Mean
G. ogac	7	431–583	492
G. morhua	6	372–772	557
G. macrocephalus	6	313–417	358
Total	19	313–772	470

TABLE 3. Comparison between the number (*P*) and the percentage of tuberculate scales from different

			a		*b*	
Species	Sex	*N*	*P*	%	*P*	%
G. ogac	♂	4	82.8 (69–96)	76.8 (64.8–100.0)	84.3[a] (46–143)	86.4[a] (76.7–92.3)
	♀	4	111.8 (92–158)	83.7 (61.3–100.0)	79.8 (54–95)	91.5 (88.5–95.3)
	♂ + ♀	8	97.3 (69–158)	80.2 (61.3–100.0)	81.7 (46–143)	89.3[b] (76.7–95.3)
G. morhua	♂	4	127.8 (89–166)	93.5 (84.8–100.0)	107.0 (63–165)	90.5 (86.3–95.9)
	♀	2	104.5 (94–115)	78.7 (71.9–85.5)	134.5 (77–192)	96.9 (96.3–97.5)
	♂ + ♀	6	120.0 (89–166)	88.6 (71.9–100.0)	116.2 (63–192)	92.6 (86.3–97.5)
G. macrocephalus	♂	3	6.0 (0–10)	7.7 (0.0–13.2)	10.0 (3–23)	17.9 (5.3–41.1)
	♀	3	3.0 (0–9)	4.1 (0.0–12.2)	10.3 (6–15)	15.1 (9.1–22.4)
	♂ + ♀	6	4.5 (0–10)	5.9 (0.0–13.2)	10.2 (3–23)	16.5 (5.3–41.1)

[a] Based on 3 specimens.
[b] Based on 7 specimens.

different positions in three species of *Gadus* (range in parentheses below the mean).

	Position					
	c		*d*		*e*	
%	*P*	%	*P*	%	*P*	%
.4[a] -92.3)	32.3 (5–53)	38.2 (7.5–65.4)	6.5 (0–26)	4.9 (0.0–19.4)	13.5 (0–34)	17.8 (0.0–47.2)
.5 -95.3)	31.0 (5–77)	32.8 (6.0–85.6)	26.3 (0–98)	23.3 (0.0–72.6)	14.3 (0–38)	24.3 (0.0–67.9)
.3[b] -95.3)	31.6 (5–77)	35.5 (6.0–85.6)	16.4 (0–98)	14.1 (0.0–72.6)	13.9 (0–38)	21.1 (0.0–67.9)
.5 -95.9)	63.3 (53–76)	75.2 (56.9–100.0)	81.0 (31–128)	58.7 (23.9–88.9)	45.8 (29–57)	61.3 (42.7–79.2)
.9 -97.5)	7.0 (4–10)	7.8 (7.1–8.4)	46.0 (45–47)	47.9 (27.6–68.1)	7.0 (5–9)	9.2 (8.8–9.6)
.6 -97.5)	44.5 (4–76)	52.7 (7.1–100.0)	69.3 (31–128)	55.1 (23.9–88.9)	32.8 (5–57)	43.9 (8.8–79.2)
.9 -41.1)	0.0 (0–0)	0.0 (0.0–0.0)	14.3 (11–18)	17.6 (8.0–25.0)	0.0 (0–0)	0.0 (0.0–0.0)
.1 -22.4)	0.0 (0–0)	0.0 (0.0–0.0)	0.0 (0–0)	0.0 (0.0–0.0)	0.0 (0–0)	0.0 (0.0–0.0)
.5 -41.1)	0.0 (0–0)	0.0 (0.0–0.0)	7.2 (0–18)	8.8 (0.0–25.0)	0.0 (0–0)	0.0 (0.0–0.0)

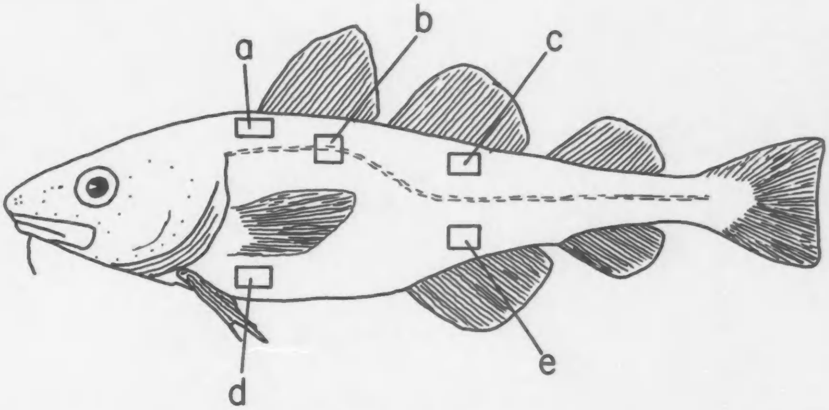


FIG. 1. Lateral view of *Gadus ogac* with the five principal areas ("squares") from which tuberculate scales and those without breeding tubercles were studied. The description of squares is given in Material and Methods.

TABLE 4. Comparison between the length of tubercles (*t*) and scales (*s*) in five tuberculate scales from one male and one female of three species of *Gadus* (range in parentheses below the mean).

	t/s (%)	
Species	♂	♀
G. ogac	8.08 (5.95–9.42)	8.29 (7.73–9.00)
G. morhua	4.16 (3.57–5.71)	3.21 (2.81–3.73)
G. macrocephalus	1.21 (0.72–1.59)	1.57 (1.45–1.79)

Description of Breeding Tubercles

Breeding tubercles are particularly noticeable on the back and flanks of *Gadus* species. On the ventral surface between the bases of the ventral fins a certain concentration of tubercles was also observed. In two females of *G. ogac*, among 124 and 126 scales, respectively 49 and 69 tuberculate scales were present. In the case of *G. morhua* a male had 135 tuberculate scales out of 238 examined, and in a female 28 tuberculate scales were observed out of a total of 130. In one mature male and one female of *G. macrocephalus* no tuberculate scales were found between the bases of the ventral fins.

Adult specimens of the three *Gadus* species display nuptial tubercles. Since tubercle terminology is ambiguous, we prefer to use the terms proposed by Wiley and Collette (1970). According to them, breeding tubercles are epidermal structures that function primarily to facilitate contact between individuals during spawning. These tubercles are typically present only on the male or are more developed on the male than on the female. As examples, we could quote the cases of Cyprinidae (Wiley and Collette 1970) or Coregonidae (Vladykov 1970).

We observed that breeding tubercles of *Gadus* consist of aggregations that appear to be nonkeratinized epidermal cells. The size of the tubercles varies with the species (Fig. 4): in *G. ogac* they are large, easily visible with the unaided eye (Fig. 2), detectable by touch, and club-shaped (Fig. 3, 4); in *G. morhua*, a magnification of at least 5× is required to see tubercles, which are horn-shaped; and in *G. macrocephalus*, still higher magnification is needed to detect the very small tubercles.

A single tubercle typically develops at the posterior edge of the cycloid scales of *Gadus*. In the case of only three specimens of *G. morhua* (two males and one female), in square *b*, 14 scales out of a total of 303 had two tubercles. The length of the scale in *Gadus* varies from 2 to 3 mm according to the size of specimens.

In our samples of tuberculate scales, it appears that no variation in number and size of tubercles exists between sexes. Thus in *Gadus*, tuberculate scales are not useful as secondary sexual characters.

Discussion

The existence of breeding tubercles in *Gadus* species has never been mentioned in the literature. The present note is based upon the study of at least 8933 scales removed from 19 specimens of three species of *Gadus*, the average per individual being 470 (Table 2).

Since the number, size, and shape of tubercles vary with the species, they can be used as taxonomic characters. As an example of the variation in the number of tuberculate scales we can use squares *a* and *b*, where tubercles are most abundant. The average percentages of tuberculate scales in positions *a* and *b* for *G. ogac* and *G. morhua* are not significantly different, but both differ dramatically from those of *G. macrocephalus* (Table 3).

The size of tubercles in absolute figures and particularly as a percentage of scale length in sexes combined differs greatly, and the ranges do not overlap between species (Fig. 4; Table 4): in *G. ogac*, 8.19%; in *G. morhua*, 3.69%; and in *G. macrocephalus*, only 1.39%.

We are not yet in a position to determine the role of tubercles in *Gadus*. If, however, they function in maintaining contact, then they should play an important role during reproduction. Unfortunately, Brawn (1961) did not notice tubercles in *G. morhua*, although she made very detailed observations on the spawning activities in this species. According to this author, during the courtship, the male makes a flaunting display of its median fins and produces grunting noises. It approaches the

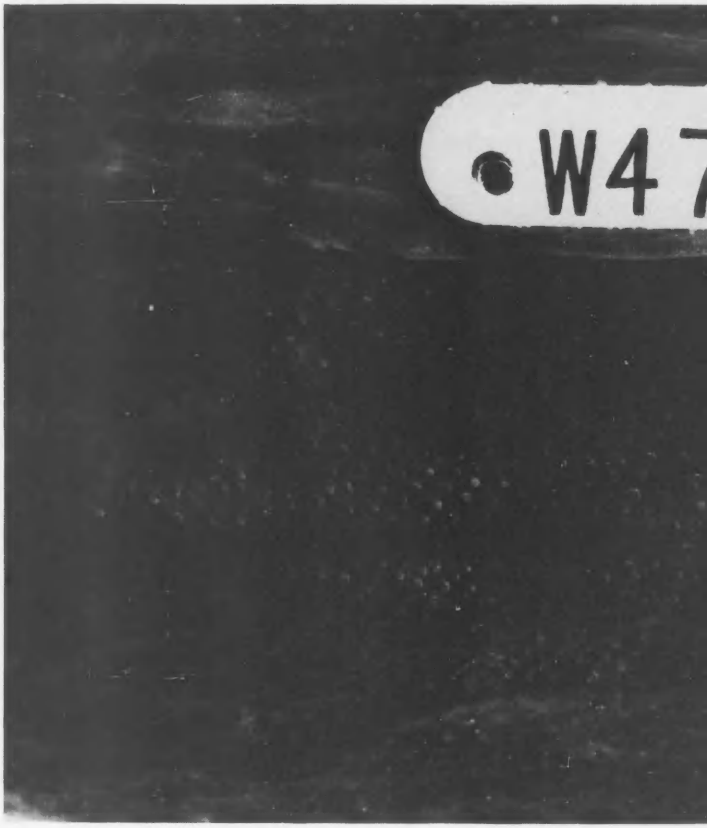


FIG. 2. *Gadus ogac* (tag W4767), spawning male, TL 490 mm from Cambridge Bay, N.
fin, around which tubercles are clearly visible.

Bay, N.W.T., 18 September 1967, collected by J. Boulva. A tag, 29 mm long, is placed on the second dorsal

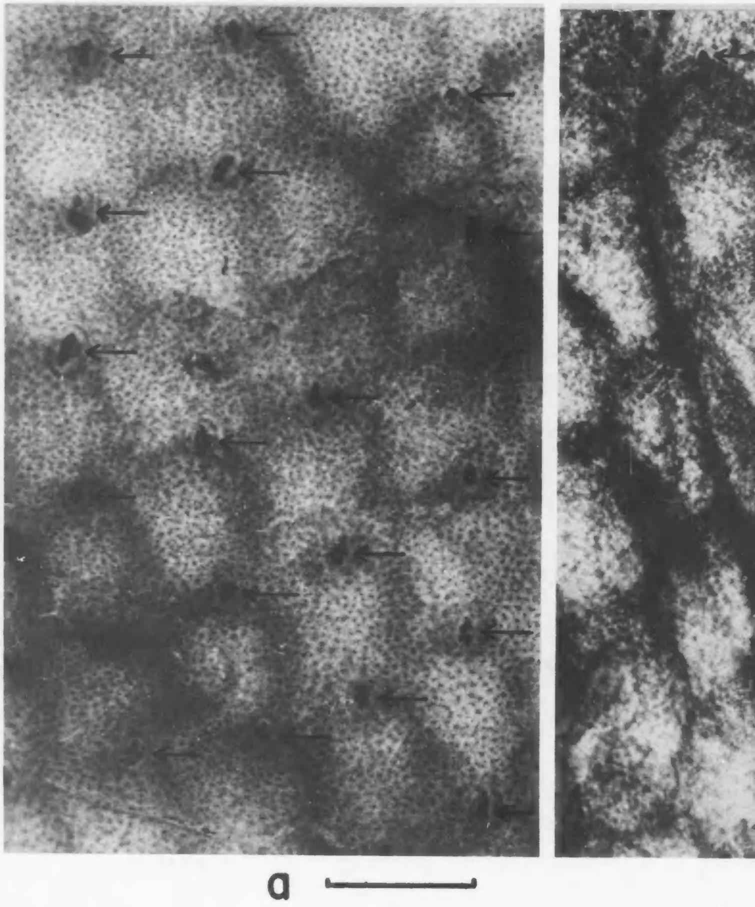
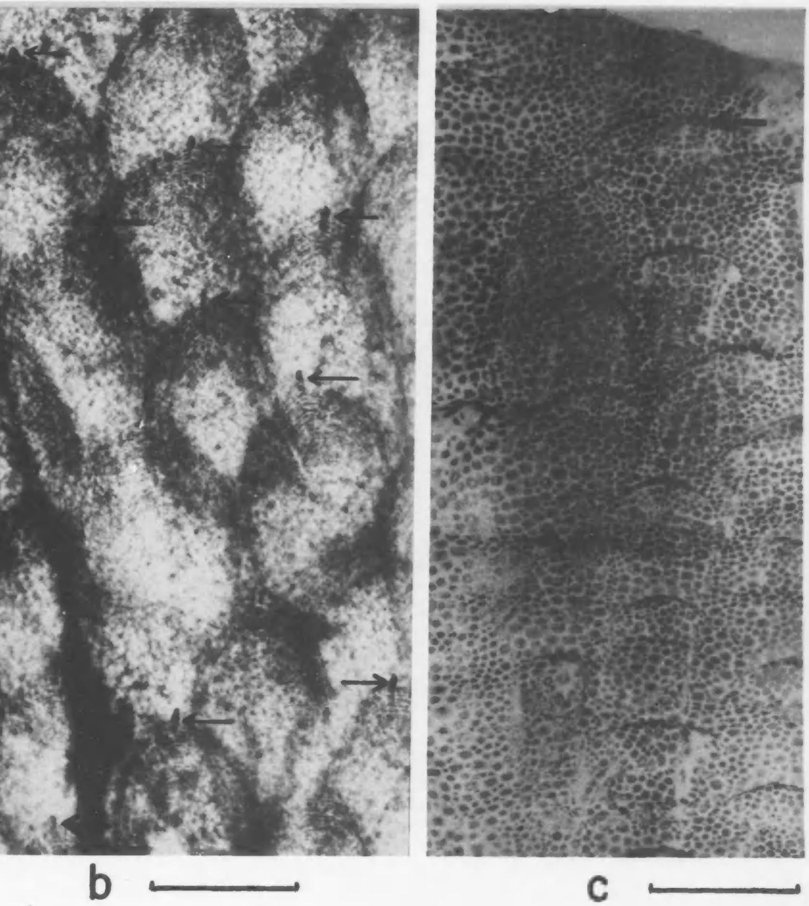


FIG. 3. Square *a* in three species of *Gadus*: (a) *G. ogac*, ♀ (tag Y4912); (b) *G. morhua*, ♂
Bar scale = 2.5 mm.



orhua, ♂ (tag Y4915); (c) *G. macrocephalus*, ♂ (tag Y4903). Arrows indicate position of tubercles.

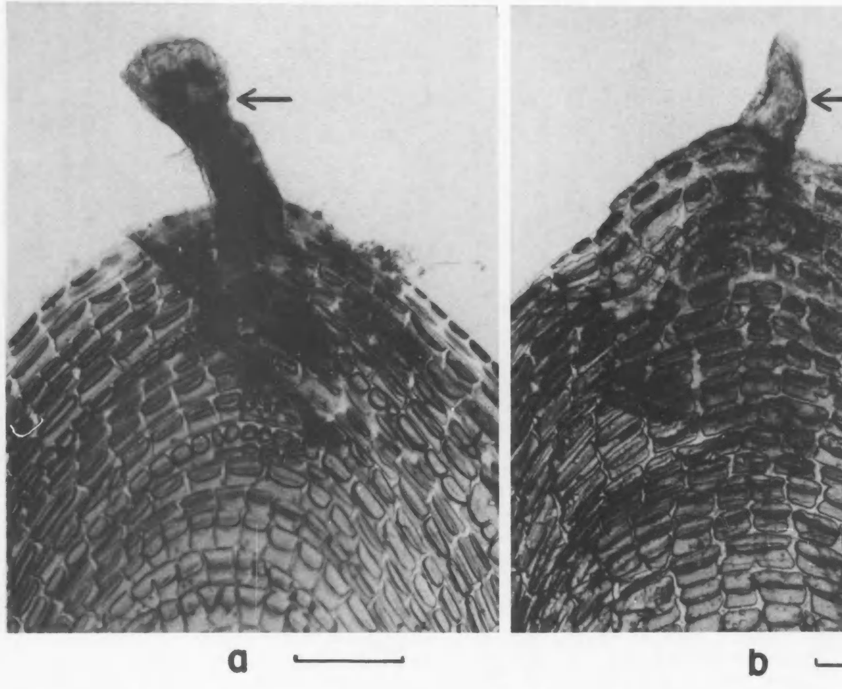
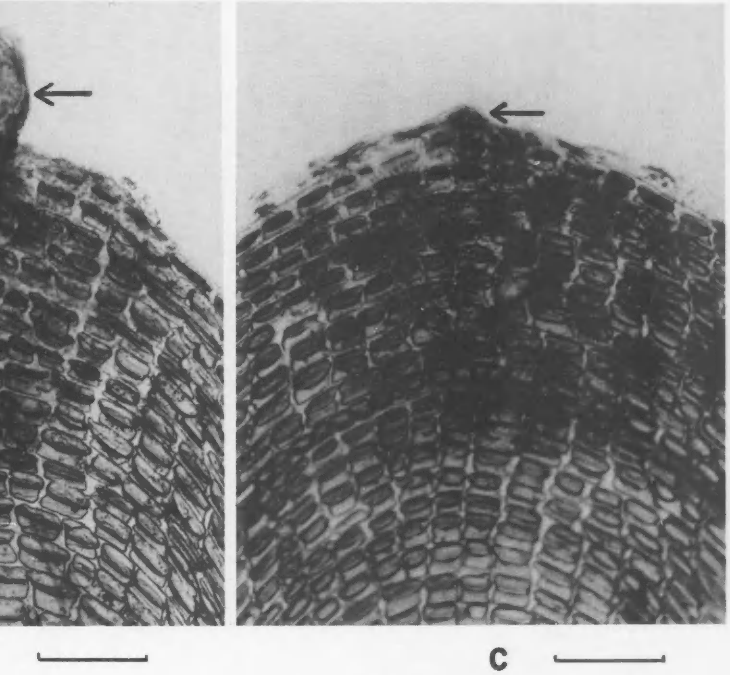


FIG. 4. Comparison between the size of tubercles from square *a* in males of three species of *Gadus*: (a
tubercle medium in length and horn-shaped; (c) *G. macrocephalus* (tag Y4905), tubercle low and very sm



adus: (a) *G. ogac* (tag Y4911), tubercle long and club-shaped; (b) *G. morhua* (tag Y4917), very small. Arrows indicate position of tubercles. Bar scale = 0.1 mm.

female from below or one side, presses the lower jaw onto the back of the female, and, pushing her downwards, swims onto her back. Once the male has mounted dorsally he immediately slips down one side of the female, still with his ventral surface closely pressed against her body. The male comes to lie in an inverted position below the female with the ventral surfaces of both fish and their genital apertures closely pressed together. Subsequently the fish spawn. The dorsal mount appears to be an essential forerunner of the ventral mount.

We believe that during close body contact (dorsal and ventral mounts), the tubercles in both sexes could play an important role.

For a better understanding of the detailed structure of breeding tubercles and their role in the reproductive cycle, the following is recommended: (1) histological study of properly preserved breeding tubercles is required; (2) more abundant material is needed to determine the size and age when breeding tubercles first develop in *Gadus*; (3) to determine whether or not tubercles of a current season are replaced by a new set in the next spawing season; and (4) establish the role of breeding tubercles in *Gadus* species during courtship and actual spawning.

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Importance of the Variation in Life History Parameters of Atlantic Salmon (*Salmo salar*)

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Atlantic salmon (*Salmo salar*) demonstrate great variability in their life history; individuals from a given year-class can spawn during several years and can, therefore, breed with salmon from other year-classes. Atlantic salmon can mature after 1–4 sea-winters and some males mature as parr, during the second through fifth years, before going to sea. Salmon may survive to spawn more than once; some spawn several times. This variability in life history may be a safeguard against loss of small stocks through several successive years of reproductive failure, since nonspawning individuals in the river or at sea could spawn in subsequent years. Spawning populations are frequently quite small. The effective spawning population size may be potentially much larger, however, since members of several year-classes, including sexually mature male parr and anadromous adults of various ages, contribute to spawning. The level of inbreeding may be relatively low, since a number of year-classes, each with different sets of parents, are represented during spawning.

Le cycle vital du saumon atlantique (*Salmo salar*) présente une grande variabilité; ainsi, des individus d'une classe d'âge donnée peuvent frayer pendant plusieurs années et donc s'accoupler avec des saumons d'autres classes d'âge. Cette espèce atteint la maturité après avoir passé de un à quatre ans en mer ; certains mâles deviennent matures à l'état de tacon, de la deuxième à la cinquième année avant la dévalaison. Le saumon peut survivre après la fraie et certains individus frayent même plusieurs fois. Cette variabilité du cycle vital peut assurer la survie des petits stocks, à la suite de la faillitte de la reproduction pendant plusieurs années successives, car les individus non reproducteurs présents en milieu fluvial ou marin peuvent frayer au cours des années suivantes. Les populations génitrices sont parfois très petites. L'effectif reproducteur peut être potentiellement plus nombreux car des membres de plusieurs classes d'âge, y compris des tacons mâles sexuellement matures et des adultes anadromes de divers âges, contribuent à la reproduction. Le taux de croisement consanguin peut être relativement faible parce qu'un certain nombre de classes d'âge produites par différents parents sont présentes au cours de la fraie.

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Recent studies in population genetics of salmonids have shown that each species includes a number of reproductively isolated populations or stocks (Møller 1970; Ricker 1972; Riddell et al. 1981; Saunders 1981). Møller (1970) suggested, and Ståhl (1980) has confirmed, that although stocks of Atlantic salmon (*Salmo salar*) are often quite small and geographically isolated as a result of individuals homing to a particular tributary or stretch along the main stem of a river, they maintain genetic diversity. Some reproductive units may have fewer than 40 pairs of anadromous parents in any spawning class. The extremely diverse life history of *S. salar* may be the mechanism that allows small populations to persist and maintain genetic diversity.

In this paper, we suggest that the great variability in age and life stage of spawners, including the presence of sexually mature male parr, allows *S. salar* to persist as small populations in which effective population size is increased by this variability, and in which the probability of inbreeding is reduced.

Results and Discussion

All possible mixtures of 1-sea-winter (grilse) and multi-sea-winter (MSW) spawners occur among Atlantic salmon stocks. The salmon populations in the Big Salmon and Restigouche rivers in New Brunswick show contrast with respect to spawning types. The Big Salmon River is relatively short, with the majority of anadromous salmon spawning initially as grilse (Table 1). Repeat (multiple) spawners comprised relatively high percentages of the spawning population during the years 1964–72; most of these spawned initially as grilse. There was always a number of year-classes represented, largely by multiple spawners. In some years there were few maiden spawners. This was the case in 1969 when most reproduction was by multiple spawners. There were, however, five year-classes present to spawn. The spawning population of the Restigouche River has fewer grilse and multiple spawners, but more MSW maiden spawners than the Big Salmon River population (Table 2). This spawning population typically includes contributions each year from six or more year-classes of anadromous fish.

Each stock of *S. salar* is an adaptation to local conditions and reflects past selection pressure. The species has a potential much broader than the life history variations described for the Big Salmon and Restigouche rivers. Table 3A shows the variation in life history of *S. salar* in the number of life stages of a given year-class present in any year and the persistence of spawning members of that year-class over time. This model, for the 1981 year-class (1980 brood year), is a composite of many *S. salar* stocks; a single stock would not likely show this range of variability. In any year there is a crop of newly hatched fry unless there has been reproductive failure. The fry develop into parr which may live in the nursery river for up to 4 yr, longer in some northern rivers such as those in the northern range of the species, e.g. Ungava Bay (Power 1961). Some male parr become sexually mature, rarely during their first year, but commonly during the next 3 yr. These mature parr contribute reproductively, some repeatedly and others only once before smoltifying and going to sea and returning as anadromous spawners (Mitans 1973; Österdahl 1969; Thorpe and Morgan 1980). Mitans (1973) and Leyzerovich (1973) presented evidence that few precocious parr reach the sea because of high overwinter mortality rates. This is reflected in a predominance of female smolts among some populations (Forsythe 1967), which leads to a predominance of female spawners. The minimum smolt age in Canadian rivers is 2 yr. In our model, there are three smolt classes from the 1981 year-class. (In southern United Kingdom, France, and Spain there are some 1- as well as 2- and 3-yr smolts (Prouzet and Jezequel 1983). Ungava smolts may be as old as 6 yr (Power 1961).) The first anadromous spawners are grilse, male and female, which return after 1 yr at sea. In our model, there are three grilse classes. Similarly, there are three successive classes of 2- and 3-sea-winter spawners. Multiple spawning offers possibilities for genetic contribution of the year-class over a number of years; some individuals may spawn as many as six times (Ducharme 1969). Our model is limited to one subsequent spawning for each class of spawners. These are separated into short and long absence which refer, respectively, to individuals spawning subsequently after 2 or more years.

In our model, the 1981 year-class persists for 10 yr. Counting mature parr, this year-class produces spawners during 9 of the 10 yr. With annual production of such year-classes, it is possible that each of the life stages will be represented each year by a number of brood years and corresponding year-classes. In any year there could be spawning representatives from as many as 10 brood years. This plasticity is derived from differences in smolt age, length of sea life before first spawning, and the possibility of multiple spawning. Such variability reduces the chance of losing the genetic contribution of any year-class.

TABLE 1. Percentage composition of five brood years of Atlantic salmon in Big Salmon River, N.B., with respect to river and sea age and multiple spawning history. Unpublished data from B. G. Jessop (DFO, Halifax, N.S., pers. comm.). Percentages do not always total 100 because of rounding errors. *G* = grilse or 1-sea-winter spawner.

		River age								Repeat spawners		
		2 sea age:			3 sea age:			4 sea age				
Brood year	(*N*)	G	2	3	G	2	3	G	Unknown %	%	Max. no. of times[a]	First time as G(%)
1964	(57)	7	16	—	33	—	—	2	5	37	4	80
1965	(118)	23	—	—	37	1	—	—	8	31	5	89
1966	(179)	39	2	—	29	—	—	—	4	27	4	100
1967	(170)	5	—	—	13	—	—	2	2	78	5	95
1968	(971)	19	3	0.3	25	3	0.5	0.5	6	44	6	87
1969	(368)	2	4	—	2	5	—	0.8	2	85	6	91
1970	(668)	19	0.6	—	19	0.8	—	—	6	54	7	85
1971	(415)	35	0.5	0.2	12	—	—	—	23	29	6	96
1972	(551)	38	1	—	31	0.4	0.2	—	24	6	5	97

[a] Maximum number of times the fish have returned to freshwater to spawn.

TABLE 2. Percentage composition of five brood years of Atlantic salmon from Restigouche River, N.B., with respect to river and sea age. There were few multiple spawners and these are not identified as to maiden spawning history. Those indicated as 4-, 5-, and 6-yr sea age probably spawned previously. Percentages do not always total 100 because of rounding errors. Data from Peppar and Pickard (1975) and Pickard and Peppar (1979).

		River age														
		2 sea age:						3 sea age:						4 sea age:		
Brood year	(*N*)	G	2	3	4	5	6	G	2	3	4	5	6	G	2	Repeat spawners
1973	(811)	7	12	4	0.1	0.1	—	8	46	17	0.9	0.1	—	1	3.7	2
1974	(1169)	8	21	3	3	—	—	28	21	9	1.5	—	—	4	0.9	2
1976	(1636)	16	10	2	1	0.2	—	26	31	7	1	0.5	—	1	3	4
1977	(964)	5	26	3	0.4	0.7	—	32	25	6	1	0.1	0.2	0.4	1.6	3
1978	(531)	—	5	7	—	0.2	0.4	24	44	10	1	4	—	3	2.3	3

A single year-class can produce as many as seven types of spawners within a spawning population, e.g. 1987 in Table 3A. Variability in life history can minimize inbreeding because there can be up to nine year-classes represented in each spawning population and three year-classes contributing as each spawning type (Table 3B). As a result, there is increased opportunity for mating among year-classes. Mature parr can mate with grilse and no other females from their own year-class but with grilse as well as all other female spawning types from nine other year-classes. The spawning population in a stock of *S. salar* is effectively a continuum, several times larger than the number of fish spawning in 1 yr.

Special attention is called to the importance of genetic contribution by sexually mature male parr. Mature males are commonly found in *S. salar* and their incidence in nature and in hatchery-reared populations is variable (Schiefer 1971; Schaffer and Elson 1975; Saunders and Sreedharan 1978; Glebe et al. 1979; Saunders et al. 1982). Mature parr participate in the spawning act and sire offspring (Jones and King 1952; Jones 1959; Österdahl 1969), although they are said to be incapable of stimulating large anadromous females to spawn (Jones 1959) They use their small size to advantage by dashing in close to the released eggs to contribute their milt (Jones 1959; Ouellet 1977; R. Porter, DFO, St. John's, Nfld., pers. comm.). Schroder and Ducker (1979) showed that satellite male chum salmon (*Oncorhynchus keta*) contribute substantially to spawning. Although dominant males fertilized more eggs, the contribution by satellite males was as high as 46%. This was determined by using genetic markers to identify biochemically the contribution of satellite and dominant males to offspring. No such studies have been done with mature Atlantic salmon parr which are much smaller than the satellite males of *O. keta*. Mature parr produce much greater volumes of milt per unit size than large, anadromous males (B. D. Glebe, Atlantic Salmon Research Institute, St. Andrews, N.B., unpubl. data), and the packed sperm volume (spermatocrit) is usually greater for parr than for large males. Mature male parr are, therefore, capable of making a substantial genetic contribution. Further studies are necessary to document the actual contribution by mature parr during individual spawning acts and the number of females with which individual anadromous and parr males spawn. We commend Atlantic salmon biologists to collect the appropriate life history data to develop models to test the hypotheses developed here that effective population size is enhanced by

TABLE 3. (A) Representation of a typical year-class[a] (1981) of *S. salar* with various life stages in a river, showing number of stages present during a single year and number of years during which the year-class persists. (B) Year-classes of Atlantic salmon represented at various life stages in the spawning population during a given year (1981). SW = sea-winter.

Year	Fry	Parr	Mature male parr	Smolt	Grilse	2-SW spawner	3-SW spawner	Grilse respawner, short absence	Grilse respawner, long absence	2-SW respawner, short absence	2-SW respawner, long absence	3-SW respawner, short absence	3-SW respawner, long absence
A.													
1981	+	+											
1982		+	+										
1983		+	+	+									
1984		+	+	+	+								
1985				+	+	+		+					
1986					+	+	+	+	+	+			
1987						+	+	+	+	+	+	+	
1988							+		+	+	+	+	+
1989											+	+	+
1990													+
B.													
1981	1980^b	1977^b	1977	1976	1975	1974	1973	1974	1973	1973	1972	1972	1971
		1978^b	1978	1977	1976	1975	1974	1975	1974	1974	1973	1973	1972
		1979^b	1979	1978	1977	1976	1975	1976	1975	1975	1974	1974	1973

[a] The term year-class as used here refers to those salmon that hatched during a particular spring. The 1981 year-class fish are from the 1980 brood year.

[b] Immature members of year-class, not included in spawning population.

variability in life history, with particular reference to mature male parr, and that multiple age at spawning reduces the probability of inbreeding.

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Temps d'ajustement de la flottabilité des saumons atlantiques (*Salmo salar*) d'élevage et flottabilité comparée de saumons atlantiques d'élevage et sauvages

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Nous avons déterminé le temps d'ajustement de la flottabilité des saumons atlantiques (*Salmo salar*) juvéniles d'élevage et vérifié si leur position plus élevée maintenue dans le plan d'eau par comparaison aux saumons sauvages pourrait résulter d'une plus grande flottabilité. Introduits dans un courant, les saumons atlantiques d'élevage ajustent leur flottabilité en moins de 24 h. Il n'y a pas de différence dans la flottabilité des saumons atlantiques juvéniles d'élevage et sauvages en milieu sans courant. Par contre, les saumons atlantiques d'élevage sont plus flottants que les saumons sauvages dans un courant. Même après avoir séjourné près de 3 mo dans une rivière, l'ajustement de la flottabilité des saumons atlantiques juvéniles d'élevage n'a pas changé. L'acquisition d'un comportement de pisciculture semble être responsable de la différence d'ajustement de leur flottabilité.

We determined the time of adjustment of buoyancy of juvenile hatchery-reared Atlantic salmon (*Salmo salar*) and investigated whether if their higher position off the substratum, compared with wild fish, might better result from a higher buoyancy. In flowing water, hatchery-reared Atlantic salmon adjust their buoyancy within 24 h. No difference in buoyancy exists between juvenile hatchery-reared and wild Atlantic salmon in still water. However, juvenile hatchery-reared Atlantic salmon are more buoyant in flowing water than wild Atlantic salmon. Even after 3 mo in a stream, the buoyancy of juvenile hatchery-reared Atlantic salmon did not change. Acquired hatchery behaviour appears to be responsible for their difference in buoyancy.

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Le saumon atlantique (*Salmo salar*) juvénile et l'omble de fontaine (*Salvelinus fontinalis*) réagissent à des changements de la vitesse du courant en ajustant leur flottabilité (Saunders 1965). Les poissons dans le courant sont plus denses que ceux qui demeurent en eau calme. Cette adaptation facilite le maintien d'une position en contact avec le fond et empêche les poissons d'être entraînés par le courant. Le temps nécessaire à l'ajustement du volume de la vessie natatoire, pour un poisson soumis à un courant, peut donc être un facteur déterminant dans le taux de réusssite des ensemencements effectués dans les rivières.

Quelques observations préliminaires effectuées par Saunders (1965) indiquent que l'ajustement de la flottabilité s'effectuerait en moins de 46 h chez les fretins d'élevage du saumon atlantique et en moins de 14 h chez les tacons sauvages. Neave *et al.* (1966) observèrent que l'ajustement de la flottabilité chez les tacons du saumon atlantique ne s'effectuait pas complètement en 24 h mais qu'un changement considérable avait lieu durant les 12 premières heures.

Dickson et MacCrimmon (1982) et MacCrimmon *et al.* (1983) ont observé que le saumon atlantique juvénile d'élevage maintient une position dans le plan d'eau juste au-dessus du substrat, position intermédiaire entre celle occupée par le saumon sauvage (au fond) et l'omble de fontaine (entre deux eaux). Sosiak (1978) observa le même phénomène lorsqu'il compara le comportement des saumons atlantiques juvéniles d'élevage avec celui des saumons sauvages. Saunders (1965) démontra que l'omble de fontaine possède une flottabilité plus élevée que le saumon atlantique juvénile, peu importe la vitesse du courant. Enfin, Sosiak (1982) observa que chez la truite brune (*Salmo trutta*), les poissons d'élevage possèdent une flottabilité plus élevée que les poissons sauvages lorsqu'ils sont maintenus dans un courant. À la suite de ces observations, il nous a semblé que la position respective maintenue dans le plan d'eau par les diverses espèces ou populations de poissons pourrait être reliée à leur flottabilité.

Nous avons tenté de déterminer avec plus de précision le temps d'ajustement de la flottabilité des saumons atlantiques juvéniles d'élevage, à la suite de leur introduction dans un courant. De plus, nous avons vérifié si la position plus élevée maintenue par le saumon atlantique juvénile d'élevage dans le plan d'eau, par comparaison au saumon sauvage, pourrait résulter d'une plus grande flottabilité. Enfin, nous avons voulu déterminer si les saumons atlantiques juvéniles d'élevage ajustent leur flottabilité comme les saumons sauvages après avoir passé un certain temps dans un milieu naturel.

Tableau 1: Fretins de saumons atlantiques utilisés pour l'évaluation de la pression de flottabilité neutre. N : nombre de spécimens, $\overline{LF}$: longueur moyenne à la fourche (cm), $\bar{P}$: poids moyen (g), $\bar{K}$: coefficient moyen de condition et σ : écart type.

Souche	N	$\overline{LF}$ (σ)	$\bar{P}$ (σ)	$\bar{K}$ (σ)
D'élevage de parents sauvages[a]	30	7,0 (0,5)	3,2 (0,7)	0,94 (0,08)
Domestique[b]	41	7,9 (0,9)	4,9 (1,7)	0,96 (0,08)
Domestique ensemencée[c]	25	7,9 (0,7)	5,0 (1,1)	0,98 (0,11)
Sauvage[d]	23	7,1 (0,4)	2,8 (0,5)	0,79 (0,05)

[a] Parents sauvages de la rivière Métabetchouane.

[b] Souche Baldwin B83-76.

[c] Souche Baldwin B83-76; ont séjourné 3 mo dans la rivière aux Saumons.

[d] Rivière aux Saumons.

Matériel et méthodes

Cette recherche a été effectuée à l'aquiculture de l'Université du Québec à Chicoutimi en 1982 et 1983. Les poissons étaient gardés en groupes de 50 à 100 individus, dans un même bassin rectangulaire de 45 cm sur 120 cm, divisé en deux par un grillage. Un évacuateur situé au centre du bassin maintenait le niveau de l'eau à 18 cm. L'eau d'alimentation provenait du système d'aqueduc de la ville de Chicoutimi et passait dans une colonne de charbon activé. Les arrivées d'eau étaient situées aux deux extrémités du bassin. Les poissons étaient soumis à une photopériode de 12:12. Une période d'acclimatation de 2 sem était donnée aux poissons avant le début des expériences. Les poissons ont été nourris quotidiennement avec du foie de boeuf.

Les expériences ont été effectuées à l'aide d'un bassin expérimental en bois semblable à celui décrit par Saunders (1965). Une pompe électrique était utilisée pour produire un courant d'une vitesse moyenne de 17 cm/s (5–31 cm/s). Les poissons étaient confinés dans une section de 61 cm de longueur, fermée à ses extrémités par un grillage, et au-dessus par une moustiquaire. L'eau était renouvelée constamment à l'extrémité amont du bassin, et le niveau de l'eau était maintenu constant à l'aide d'un trop-plein à l'autre extrémité.

Le matériel utilisé pour mesurer la pression de flottabilité neutre est semblable à celui décrit par Saunders (1965). Le volume de la vessie natatoire, et par conséquent la densité du poisson, peut être modifié en faisant varier la pression. Un poisson anesthésié est inséré dans un récipient fermant hermétiquement. Un vide partiel est fait dans le contenant et la réduction de la pression est mesurée avec un manomètre au mercure. On diminue la pression jusqu'à ce que le poisson se maintienne entre deux eaux. La pression atmosphérique moins la réduction de la pression nécessaire pour que le poisson flotte entre deux eaux donne la pression de flottabilité neutre. Plus un poisson est flottant, plus sa pression de flottabilité neutre est élevée. Les poissons étaient capturés individuellement à l'aide d'une puise et transférés dans un récipient de 4 L contenant 10 cm d'eau. Les poissons étaient anesthésiés avec du MS-222 (Sandoz), méthane sulfonate de tricaïne. Une pompe à vide électrique était utilisée pour réduire la pression dans le récipient. Les poissons ayant expiré du gaz de leur vessie natatoire étaient éliminés. Par la suite, les poissons étaient transférés dans un bassin de récupération, avant d'être remis dans leurs bassins de rétention respectifs.

L'étude du temps d'ajustement de la flottabilité a été faite entre le mois d'octobre 1982 et le mois de mars 1983, à une température variant de 14 à 3°C. La pression de flottabilité neutre a été mesurée chez des fretins (0+) en eau calme, puis d'autres fretins ont été soumis à un courant pendant 5, 30 et 45 min, et 1, 3, 6, 12, 24, 48 et 120 h. La pression de flottabilité neutre a été également mesurée chez des fretins ayant passé 12 h dans le courant et qu'on a empêché de remonter à la surface de l'eau par un grillage. De 6 à 21 individus différents étaient utilisés à chaque intervalle de temps. Les valeurs moyennes de la pression de flottabilité neutre ont été comparées au moyen d'un test de Student. Les fretins de saumons atlantiques provenaient de géniteurs, des ouananiches (saumons d'eau douce), capturés dans la rivière Métabetchouane (tributaire du lac Saint-Jean) à l'automne 1981. Les oeufs ont été incubés et les jeunes saumons élevés à la pisciculture de Tadoussac. Les caractéristiques des fretins utilisés sont données au tableau 1.

L'étude de la flottabilité comparée des saumons atlantiques d'élevage et des saumons sauvages a été effectuée en 1983, du mois d'octobre au mois de novembre, la température de l'eau variant de 16 à 9°C. La pression de flottabilité neutre a été mesurée chez les fretins, après qu'ils eussent été maintenus dans un milieu d'eau calme et, ensuite, après un séjour de 24 h dans le courant. Nous avons utilisé le même test que précédemment pour comparer nos résultats. Pour cela, 24 fretins de saumons atlantiques sauvages d'eau douce ont été capturés, à l'aide d'une pêche électrique, le 29 septembre 1983, dans la section aval de la rivière aux Saumons (tributaire du lac Saint-Jean). Le même jour, 26 fretins de saumons atlantiques d'eau douce de la souche domestique de Baldwin, ayant été ensemencés dans la section amont de la rivière aux Saumons le 29 juin 1983, ont été également capturés. Il est à noter que deux chutes infranchissables empêchent les saumons sauvages d'accéder à la section amont de la rivière où les fretins domestiques avaient été ensemencés. Provenant de la souche domestique de Baldwin, 45 fretins ayant été élevés à la pisciculture privée La Baie Enr., ville de La Baie, ont été transférés à l'aquiculture de l'Université du Québec à Chicoutimi le 5 octobre. Les caractéristiques des différents échantillons sont données au tableau 1.

Résultats

Nous obtenons une diminution significative ($P < 0{,}02$) de la pression de flottabilité neutre des fretins, 30 min après leur introduction dans un courant. Les valeurs moyennes de la presssion de flottabilité neutre demeurent moins élevées ($P < 0{,}01$) chez les fretins maintenus dans un courant, par comparaison avec ceux maintenus en eau calme, pour des périodes allant de 1 à 120 h (12 h, $P < 0{,}05$).

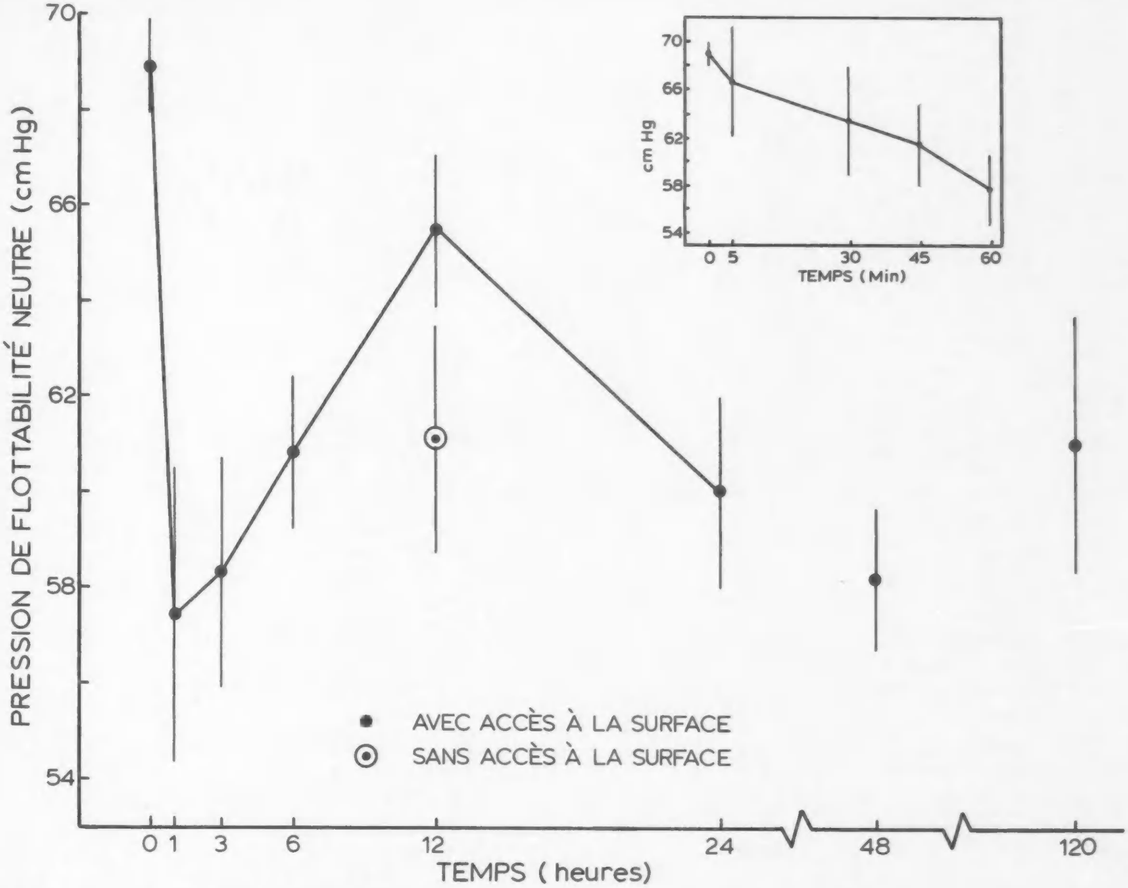

FIG. 1. Variation de la pression de flottabilité neutre des fretins d'élevage de parents sauvages de la rivière Métabetchouane, à la suite de leur introduction dans un courant. Les intervalles de confiance à 95 % sont représentés par les traits verticaux.

La figure 1 montre comment l'ajustement de la flottabilité s'effectue, à la suite de l'introduction de fretins d'élevage dans un courant. L'ajustement se fait en trois étapes. Nous observons une diminution rapide mais graduelle de la valeur moyenne de la pression de flottabilité neutre d'une durée d'environ une heure. Cette diminution de la flottabilité est suivie d'une augmentation importante s'échelonnant sur une période d'environ 12 h pour ensuite redescendre et se stabiliser 24 h après l'introduction. Ces valeurs sont significativement différentes ($P < 0,01$).

Si nous empêchons les fretins d'avoir accès à la surface, la valeur moyenne de la pression de flottabilité neutre obtenue après 12 h est moins élevée ($P < 0,01$) que lorsqu'ils ont accès à la surface.

Les fretins sauvages et d'élevage diminuent leur flottabilité ($P < 0,01$) lorsqu'ils sont introduits dans un courant (fig. 2). Il n'y a pas de différence significative ($P > 0,05$) entre la flottabilité des fretins d'élevage et sauvages, lorsqu'ils sont dans un milieu où il n'y a pas de courant. Par contre, dans un courant, les fretins d'élevage ont une plus grande flottabilité ($P < 0,01$) que les fretins sauvages. De plus, même après que les fretins d'élevage eurent séjourné près de 3 mo dans un milieu naturel, où la vitesse du courant était de 18–60 cm/s, l'ajustement de la flottabilité n'a pas changé significativement ($P > 0,05$).

Discussion

Les variations de la pression de flottabilité neutre des fretins d'élevage de saumons atlantiques, à la suite de leur introduction dans un courant (fig. 1), correspondent aux observations de comportement qu'effectua Sosiak (1978) sur des saumons atlantiques juvéniles d'élevage. Cet auteur mentionne que lorsqu'ils étaient introduits dans une rivière artificielle, les saumons coulaient au fond. Après 15 à 30 min, quelques individus nageaient vers la surface et semblaient avaler de l'air. Par la suite, ces individus nageaient au-dessus du fond.

Les physostomes peuvent diminuer la quantité de gaz de leur vessie natatoire en l'expirant et, selon Verheijen (1962), ce comportement peut être provoqué par un stress quelconque. Ainsi Rimmer (1975) observe une diminution importante de la flottabilité des fretins de saumons atlantiques après leur transport de la pisciculture aux lieux d'ensemencement. Les saumons atlantiques juvéniles d'élevage introduits dans un courant diminueraient rapidement leur flottabilité en expirant du gaz de leur vessie natatoire à cause du stress provoqué par le nouveau milieu. Cette diminution ne s'effectue pas instantanément, mais graduellement (fig. 1). Par la suite, ceux-ci rempliraient leur vessie natatoire en avalant de l'air à la surface, puisque

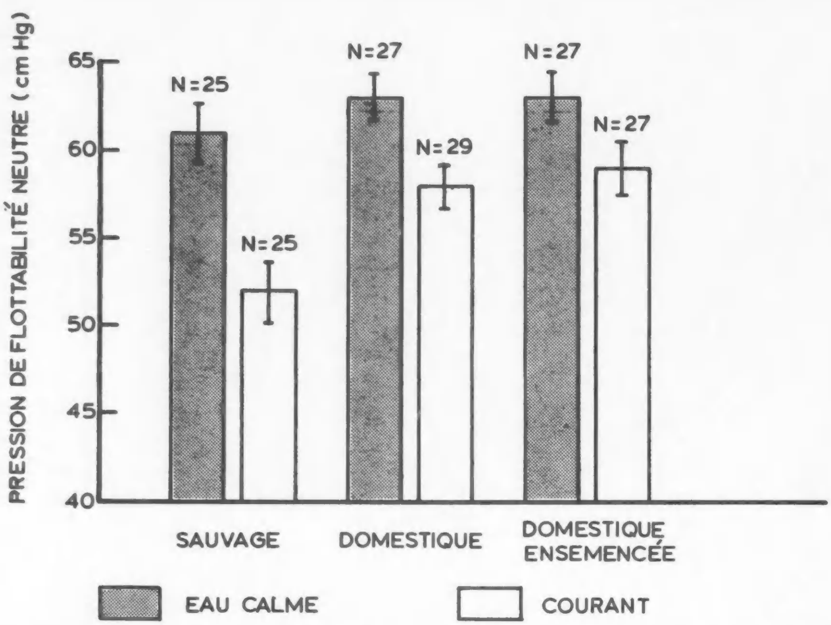

FIG. 2. Pression de flottabilité neutre moyenne des fretins de saumons atlantiques en eau calme et après qu'ils ont séjourné 24 h dans un courant. Les intervalles de confiance à 95 % sont représentés par des traits verticaux et le nombre d'invididus par *N*.

l'augmentation de la flottabilité observée après 12 h est inhibée si on les empêche d'avoir accès à la surface. Finalement, ils ajusteraient leur flottabilité en fonction des nouvelles conditions du milieu en moins de 24 h. Le temps d'ajustement « final » correspond assez bien avec ce que rapportent Neave *et al.* (1966) pour le temps d'adaptation des tacons, mais la période d'adaptation est beaucoup plus courte que celle mentionnée par Saunders (1965) pour les fretins.

Quatre causes nous semblent possibles pour expliquer la différence de flottabilité entre les fretins sauvages et d'élevage lorsqu'ils sont exposés à un courant. Cette différence pourrait être causée par une densité différente des tissus, par une morphologie différente, par une sélection génétique ou par l'acquisition d'un comportement de pisciculture.

La densité des tissus peut être affectée par son contenu en lipides et ainsi modifier la flottabilité ; d'ailleurs le coefficient de condition diminue lorsque le contenu en lipides devient plus faible (Pinder et Eales 1969). Nos fretins d'élevage avaient effectivement un coefficient de condition (tableau 1) plus élevé ($P < 0{,}01$) que les fretins sauvages. Bergström (1973) a également trouvé un contenu en lipides plus élevé chez des saumons atlantiques d'élevage que chez des saumons sauvages. Cependant, Pinder et Eales (1969) ont mentionné qu'il n'y a pas de corrélation entre la pression de flottabilité neutre et la densité des tissus, qui à son tour, n'est pas significativement corrélée avec la quantité de graisse que l'on peut extraire à l'éther. Enfin, Sosiak (1982) mentionne que la densité ne semble pas déterminer l'ajustement de la flottabilité, puisque ses truites brunes avaient la même densité que ses saumons atlantiques, et qu'ils avaient une flottabilité différente. Il semble donc peu probable que la densité des tissus puisse jouer un rôle important dans la différence de la flottabilité. On pourrait penser que la morphologie peut contribuer à déterminer la position du saumon dans un plan d'eau. Cependant, lors de la smoltification, les saumons se maintiennent entre deux eaux (Evropeitseva 1959) et ils acquièrent une flottabilité plus élevée (Saunders 1965 ; Pinder et Eales 1969). Pourtant, ils devraient se tenir au fond puisqu'ils deviennent plus élancés en diminuant leur coefficient de condition (Pinder et Eales 1969).

Les poissons élevés en pisciculture sont exposés à une sélection génétique artificielle (Smith 1961). Cette sélection peut amener un changement du comportement des poissons (Vincent 1960). Or, nos résultats démontrent que les poissons de souche domestique exhibent le même type de comportement que les poissons provenant d'oeufs de parents sauvages (Sosiak 1982). Il est donc peu probable qu'une sélection génétique soit responsable d'un tel changement de comportement dans un laps de temps si court.

Comme nos résultats l'indiquent, des saumons ayant séjourné en milieu artificiel pendant une courte période voient leur comportement modifié même après un long séjour en milieu naturel. Ritter et MacCrimmon (1973) ont démontré que les conditions environnementales modifiaient le comportement des truites arc-en-ciel (*Salmo gairdneri*) de même origine lorsqu'elles étaient exposées à des conditions différentes durant 6 mo, même si elles avaient été élevées dans des conditions identiques durant les cinq premiers mois de leur vie et remises dans les conditions premières pendant une période de 2 mo. Smith (1961) mentionne étalement qu'une courte période passée dans un milieu artificiel peut modifier le comportement des poissons. Les conditions environnementales en pisciculture, étant différentes de celles rencontrées dans la nature, pourraient donc expliquer les réponses différentes des deux groupes de poissons face à une augmentation de la vitesse du courant. Les fretins sauvages du saumon atlantique sont soumis à des conditions environnementales variées, ce que les fretins d'élevage ne rencontrent pas en pisciculture. Ceci pourrait expliquer que la différence de flottabilité ne se manifeste que lorsque les poissons sont soumis à un courant. De plus, même après que les fretins d'élevage de souche domestique ont passé 3 mo dans un milieu naturel, l'ajustement de la flottabilité reste le même, ce qui est en accord avec Ritter et MacCrimmon (1973).

En conclusion, le temps d'ajustement de la flottabilité étant très court, ce facteur ne devrait pas influencer d'une façon importante le taux de réussite des ensemencements effectués dans les rivières. De plus, l'acquisition d'un comportement de pisciculture semble être responsable de la différence d'ajustement de la flottabilité des saumons atlantiques juvéniles d'élevage. En conséquence, une flottabilité plus élevée pourrait amener les saumons atlantiques d'élevage à nager plus près de la surface que les saumons sauvages, ce comportement ayant été observé par Sosiak (1978), Dickson et MacCrimmon (1982) et MacCrimmon *et al.* (1983). Les saumons d'élevage doivent donc lutter contre une vitesse de courant plus élevée, augmentant ainsi leur dépense d'énergie et diminuant d'autant leur efficacité dans les sections d'eau vive.

Remerciements

Cette étude a été faite grâce à une bourse d'études du programme pour la formation de chercheurs et d'action concertée (FCAC). Nous remercions la direction régionale du Saguenay/Lac Saint-Jean du ministère du Loisir, de la Chasse et de la Pêche pour nous avoir fourni les ouananiches d'élevage ainsi que le matériel nécessaire à la capture des ouananiches en rivière. M. Yvon Maranda ainsi que les techniciens de l'Université du Québec à Chicoutimi nous ont aidé à garder en bonne condition les ouananiches à l'aquiculture ; nous les en remercions.

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BOOK REVIEWS/COMPTES RENDUS

A Manual of Chemical and Biological Methods for Seawater Analysis. *T. R. Parsons, Y. Maita, and C. Lalli. Pergamon Press, Oxford. 1984. 173 p. $8.95 U.S.*

The precursor of this manual, Strickland and Parsons (1972), is a standby of students and biological oceanographers for the chemical analysis of seawater. In this updated version the orientation has been changed to reflect a stronger biological interest.

The book is organized into sections giving methods for nutrients, soluble organic material, particulate matter, plant pigments, photosynthesis, bacteria, gasses in seawater, and media, preservatives, and enumeration methods for organisms. Where instruments such as salinometers and autoanalyzers exist to measure specific properties directly, methods are not included. The authors are deliberately conservative and avoid controversial techniques. For example, no method is given for dissolved organic carbon, in view of questions about the reliability of available techniques, and new methods for measurement of phytoplankton growth rates, such as DNA replication rates, are not introduced.

The manual is strictly limited to methods. Interpretation of results is not discussed, although references are given in some cases. The layout is consistent and clear for each method. An introduction giving the source is followed by sections providing range and precision, outline of the method, special equipment and apparatus, sampling procedure and storage, reagents, experimental procedure, and calibration. Notes on interfering substances, critical details of the technique, and unusual features are provided.

In comparison with Strickland and Parsons (1972), the methods for inorganic nutrients have been pared down. There is no detailed discussion of the various forms of phosphorus in seawater, for example, and a single method is given for phosphate. Methods for metal micronutrients such as iron, manganese, and copper have been eliminated. Only one vitamin, vitamin B_{12}, is dealt with as an example of bioassay technique, although references are given to similar techniques for thiamin and biotin.

The confusing mass of formulae for spectrophotometric determination of chlorophylls has been eliminated and the authors have settled on the equations of Jeffrey and Humphrey (1975). These equations are the most successful in separating the forms of chlorophyll and are becoming accepted as standard. Users freezing filtered chlorophyll samples, as suggested in the manual, would be advised to check the loss of sample introduced in this technique. A recommendation on types of glass fiber filters to use would be helpful, as some types do not completely retain all forms of phytoplankton.

The inclusion of the section on electronic sizing of particles seems out of place in a manual devoted to simple methods. The instrumentation is expensive and interpretation for field samples requires considerable skill and self-confidence. The technique for measuring sinking rates of particles is interesting but may find limited usage. Also interesting is the recommendation of a spectrophotometric method for routine oxygen analysis, with the Winkler titration reserved for absolute standardization of the method. The colorimetric technique is considered to provide better precision, sensitivity at low concentrations, and speed.

Users of a manual such as this may tend to apply methods uncritically. A large degree of trust is placed in the authors to note pitfalls. There are a few problems, as the notes about chlorophyll analysis above indicate. Investigators preserving phytoplankton samples with the recipe given for Lugol's solution will find their coccolithophorids dissolving. In general, however, the manual provides extensive annotation of methods. It is well organized and straightforward to use. Many copies are sure to become grimy and tattered with use.

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(R589)

A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters. *John A. Downing and Frank H. Rigler (editors). Blackwell Scientific Publications, Palo Alto, CA. 2nd ed. 1984. $55.00 U.S.*

When a second edition (especially a complimentary copy) crosses my desk, I tend to respond as did Disraeli upon receiving a proud friend's newly printed book: "Many thanks for your book" he wrote, "I shall lose no time in reading it." With the advent of the second edition of IBP Handbook 17, we should lose no time *before* reading it.

It is not often that a second edition is a marked improvement over a first. Like the change from first to second copepodite, it may grow a bit and add the odd appendage, but overall its appearance remains the same. Occasionally a second edition undergoes a minor metamorphosis, resembling say the difference between nauplius 6 and copepodite 1. The second edition of IBP Handbook 17 has evolved radically; in comparison, edition 1 is a protostome and edition 2 is a deuterostome — the whole body symmetry and arrangement of parts has been changed to produce a new book. Secondary production is now actually considered second (Chapter 2) instead of being relegated, almost as an afterthought, to the end of the volume as in the first edition.

The Riglerian philosophy of "the fewer authors the better" has obviously paid off. This is not to denigrate the contributions of the original authors, it is simply that the presentation and direction of the second edition is far more cohesive. Apart from a few of the original authors only the colour of the cover remains, and since the whole concept of "filter feeding" has been revised since edition 1, even the book's cover illustration has been changed!

Viewed in retrospect, the original volume was a polyglot collection of enthusiastic review, "bright ideas," and obvious technique. For example, in the mark and recapture section we were advised to "... paint numbers on the shells of molluscs"! Despite the several and collective peculiarities, and the fact that edition 1 simply didn't "hang together," it did contain much useful reference material along with its trivia. In the second edition, the reference material is thoroughly updated, and the personal trivia is largely removed. Gone are the photographs of beloved baubles; substituted are useful line drawings and diagrams.

Although in many cases our traditional sampling apparati have not changed much since edition 1, our knowledge of how they work (biases, accuracy, precision) has increased considerably. One of the most useful features of edition 2 is that it is not just a compendium of methods to sample, assess, or calculate things, but that there has been a concerted attempt to evaluate sources of experimental and observational error. The chapters are still variable in quality; traditional, primarily methodological chapters are still present (e.g. those on zooplankton sampling, lake benthos, stream benthos, and insect emergence) but at least two of these attempt to quantify biases. Many of the subjects have been more exhaustively considered elsewhere in more specialised volumes, but in a "manual" such as this we must expect a less than comprehensive treatment.

In view of the substantial improvements over the first edition, the shortcomings of the second edition tend to go unnoticed on first reading. On reexamination there were some surprises, for example: the overly long treatment of the ancient Clarke–Bumpus sampler; no mention of the two excellent UNESCO monographs on zooplankton sampling and preservation; no consideration of the sogenannt physiological methods of estimating secondary production; etc. All the authors are aware of sources of error, but it finally became irritating to be constantly reminded (at least once by each author) that "... any investigation must be tailored to the hypotheses to be tested."

When a book is written by several authors it is difficult to avoid a "chapter by chapter" analysis, but several of them emerge as clearly superior to their first edition analogs. In Chapter 2 (from Frank Rigler's original notes) the authors' style is concise and clear. It takes steady aim at its objectives whilst wending its way through a plethora of apparently puzzling production processes. These, as we are gently reminded, really reduce to different ways we can choose to calculate the same thing "at our whim." Although according to the authors, "The final calculation of production is the simplest job that the production biologist has to do", it is only recently commonplace to see estimates of secondary production in the literature, and one can run into considerable troubles along the way! Chapter 7 on abundance and biomass of zooplankton is an excellent review of a seemingly simple subject. Treatment of image analysis systems, which will surely dominate the data processing business, is especially useful, as are the cautions on estimating volumes and biomasses from limited data and unproven relationships.

It is unreasonable to ask any author for *a chapter* on statistical methods and sampling and experimental design. With inumerable textbooks on the market any single chapter must appear selective and irregular. There are several similarities between the current offering and the original chapter by Morrison Cassie (who seemed to be the only aquatic ecologist writing chapters on statistics thirteen years ago), and some of the material is dated. Statistical colleagues who reviewed the chapter found several oversights and errors of terminology. Now that most ecologists are reasonably "statistically converted" a single sermon is clearly inadequate.

Chapters 9 (feeding, grazing, and assimilation) and 10 (respiration) are far superior to the original treatments; both are excellent up-to-date reviews. However, it is incredible that we still need to be reminded to reduce our data to common and useful terms, e.g. "... express ingestion rate in terms of ... biomass ... dry weight, ... energy content, etc." Perhaps this is why ecology progresses slowly compared to other disciplines — we all speak different nontranslatable languages? Where subjects are not covered in detail (e.g. the demerits of various electivity/selectivity indices) in these chapters the reader is usually directed to a recent review.

The second edition of IBP Handbook 17 is a "secondary producer's *vade mecum*"; for those of us who knew Frank Rigler and benefitted from his argument (especially when he told us what our data really meant) it will be a prized remembrance.

Finally, if the reader is tempted to find further fault, one should consider that this is essentially a "cookbook" of methodology. Here and there an ingredient is misplaced (e.g. forward references to nonexistent chapter sections), but overall it is one of the best collections of recipes to be had.

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(R608)

BIBLIOGRAPHIA. *C.-t. Shih, D. Laubitz, and I. Sutherland (editors). National Museum of Natural Sciences, Ottawa, Canada. Vol. 1–3. Gratis to libraries and scientific workers.*

The Invertebrate Zoology Division of the National Museum of Natural Sciences, Ottawa, Ontario, Canada, has initiated what promises to be a very valuable series of publications: *Bibliographia Invertebratorum Aquaticorum Canadensium*. To date, three volumes have appeared, a fourth is in press, and others are either in preparation or are planned.

All volumes will be based upon a computerized literature survey, listing the scientific names of all aquatic invertebrates that have been recorded from Canadian waters (including non-Canadian waters in Puget Sound and the Laurentian Great Lakes, as well as also the waters of Alaska). Both marine and inland habitats are dealt with, including wetlands. All textual material is given both in English and French.

Volume 1 (*Index Generum*. 1983; prepared by D. R. Laubitz, I. Sutherland and N. Sharma; 56 p.) lists all genera of aquatic invertebrates that have been recorded in the surveyed literature, including obsolete ones (e.g. *Anuraea* and *Actinotrocha*). First, an alphabetical list is provided, each genus being identified as to the phylum, class, etc., to which it belongs. A second list is given of the genera reported in each separate phylum. Omitted are aquatic insects and the Protozoa.

Volume 2 (*Index Bibliographicus*. 1983; prepared by N. Sharma, D. R. Laubitz, I. Sutherland, P. Adams, and C.-t. Shih; 238 p.) contains an alphabetical listing (by author) of approximately 5000 papers, books, etc., that have been searched. The earliest is dated 1819, and the search has covered literature through 1976. No claim is made for completeness; the greatest omission is for marine zooplankton references prior to 1970, which have been covered previously in another museum publication.

Volume 3 (*Synopsis Speciorum. Rotifera*. 1984; prepared by R. Chengalath; 102 p.) is the first of the remaining volumes, all of which will deal with selected phyla or small groups of higher taxa. All generic plus specific names that have been recorded from Canada, including obsolete names, misspellings, typographical errors, and obvious "goofs," are listed in an index. The index leads the reader to pages in the main body of the publication, where these names are referred to the proper terminology. No attempt is made to judge whether the authors' identifications have been accurate. For each species the broad habitat is recorded, as well as the regions from which it has been reported. For freshwater species this means the provinces and territories, and for marine species the Atlantic, Pacific, or Arctic. A compilation of the references in which it has been reported, as listed in Volume 2, is given separately for each region, and also for topics such as ecology, life history, morphology, etc. Because Volume 2 lists publications only through 1976, Volume 3 also includes a bibliography of more recent papers (to 1983).

As a guide to the literature, this series will be invaluable to taxonomists, ecologists, and biogeographers, especially those interested in Canada and adjacent regions. The National Museum of Natural Sciences is to be commended for its sponsorship of the series, and we can only hope for a completion of all its volumes as rapidly as feasible. Workers interested in such subjects as physiology, morphology, genetics, etc., also will find the listed literature useful, but inevitably for them the works will be parochial because references are not given covering these subjects as investigated elsewhere in the world.

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(R609)

ANNOUNCEMENTS/AVIS

Advanced Study Institute on Physiological Ecology of Photosynthetic Picoplankton in the Ocean

San Miniato, Italy

October 1985

An Advanced Study Institute, sponsored by the NATO Scientific Affairs Division, will be held in San Miniato (near Florence), Italy, during early October 1985. The Organising Committee is as follows:

Dr. Trevor Platt (Canada), Chairman
Dr. Robert Guillard (USA)
Prof. Noel Carr (UK)
Dr. William Li (Canada)
Dr. Luigi Lazzara (Italy)
Dr. Giuseppe Magazzu (Italy)

The discussions will deal with ultrastructure, biochemistry, physiology, ecology, distribution, abundance, and contribution to marine productivity of prokaryotic and eukaryotic photosynthetic picoplankton (sensu lato).

Invited speakers are Prof. J. Raven (UK), Dr. J. Waterbury (USA), Prof. H. Thomsen (Denmark), Prof. N. Carr (UK), Prof. L. Brand (USA), Dr. T. Platt (Canada), Dr. W. Li (Canada), Dr. I. Joint (UK), Dr. M. Silver (USA), Prof. S. Chisholm (USA), Dr. L. Murphy and Dr. W. Zevenboom (Netherlands), Dr. J. Kirk (Australia), and Dr. A. Morel (France).

The Study Institute is primarily tutorial in scope, but there will be a certain amount of time allowed for short contributions that are relevant to the topics treated by the invited speakers.

Total attendance at the meeting is limited. Those interested in participating should contact Dr. Trevor Platt, Marine Ecology Laboratory, Bedford Institute of Oceanography, Box 1006, Dartmouth, Nova Scotia, Canada, B2Y 4A2. Telephone: (902) 426-3793. Telex: 01931552.

Conférence d'études avancées sur l'écologie physiologique du picoplancton végétal en milieu océanique

San Miniato (Italie)

Octobre 1985

Une conférence d'études avancées, parrainée par la Division des affaires scientifiques de l'OTAN, sera tenue à San Miniato (près de Florence), en Italie, au début d'octobre 1985. Le comité organisateur regroupe les personnes suivantes :

Dr. Trevor Platt (Canada), Président
Dr. Robert Guillard (É.-U.)
Prof. Noel Carr (R.-U.)
Dr. William Li (Canada)
Dr. Luigi Lazzara (Italie)
Dr. Guiseppe Magazzu (Italie)

Les discussions porteront sur l'ultrastructure, la biochemis, la physiologie, l'écologie, l'aire de répartition et l'abondance du picoplankton végétal procaryote et eucaryote (sensu lato) ainsi que sa contribution à la productivé marine.

Les conférence invités sont : Prof. J. Raven (R.-U.), Dr. J. Waterbury (É.-U.), Prof. H. Thomsen (Danemark), Prof. N. Carr (R.-U.), Prof. L. Brand (É.-U.), Dr. T. Platt (Canada), Dr. W. Li (Canada), Dr. I. Joint (R.-U.), Dr. M. Silver (É.-U.), Prof. S. Chisholm (É.-U.), Dr. L. Murphy et Dr. W. Zevenboom (Pays-Bas), Dr. J. Kirk (Australie) et Dr. A Morel (France).

Quoique cette Conférence d'études comporte surtout des travaux dirigés, une certaine période sera allouée à de courtes présentations connexes aux sujets traités par les conférenciers invités.

Le nombre de participants à la réunion est limité. Les personnes intéressées à y assister doivent communiquer avec le Dr. Trevor Platt, Laboratoire d'écologie marine, Institut d'océanographie de Bedford, C.P. 1006, Dartmouth (Nouvelle-Écosse), Canada B2Y 4A2. Téléphone : (902) 426-3793. Télex : 01931552.

COMING NEXT MONTH/À PARAÎTRE LE MOIS PROCHAIN

Articles

Fish gill structural changes induced by toxicants and other irritants: a statistical review **J. Mallatt**

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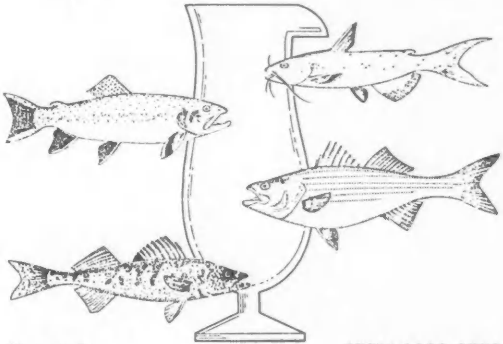

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